UNIVERSITY OF THE WITWATERSRAND

FEEDING ECOLOGY OF BIRDS IN A MIST BELT FOREST IN SOUTH AFRICA

Samantha Lüise Scott 0600598G

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Declaration

I declare that this dissertation is my own unaided work, and was conducted under the supervision of Dr. Craig T. Symes and Prof. Andrew E. McKechnie. Submission is for the degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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Samantha Lüise Scott

29 day of OCTOBER 2012

Supervisors

Dr. C.T. Symes

Prof. A.E. McKechnie

Postgraduate Research Committee

Prof. G.J. Alexander (Chair)

Dr. C.T. Symes

Prof. A.E. McKechnie

Abstract

Food is not always readily available and therefore an important limiting resource to birds. South African forests have a similar fruiting and flowering phenology to tropical forests in that food availability fluctuates over space and time. South African indigenous forest is naturally fragmented in a non-forest matrix and therefore differs from tropical forests. Anthropogenic landuse change has contributed to the increased fragmentation of indigenous forest. The isolated nature of patches provides a suitable platform from which to assess changes in a forest bird community between seasons because they are structurally and functionally distinct from the surrounding vegetation. Therefore, the aim of the study was to assess food as a driver of community dynamics and dietary patterns of birds in a Mist Belt Mixed *Podocarpus* forest patch between two distinct seasons, winter and summer. This was assessed through a combination of field techniques and stable isotope analysis of carbon and nitrogen. Further, birds were categorised as forest specialists, forest generalists, and forest visitors based on published information to provide extra insight into community changes. Species richness and abundance differed between seasons due to the local movements and turnover of birds and due to the influx of migrants into the forest. In addition, nectarivores and frugivores increased in abundance and biomass in the forest in winter when flowers and fruit were readily available from canopy trees, such as *Halleria lucida* and *Podocarpus latifolius*. However, insect-eating guilds increased in summer when there was a greater diversity of invertebrates. Nectarivores, granivores, and omnivores vertically tracked food within forest height strat to where it was most abundant, demonstrating a close association with the location of their food resources. Further, the niche of several species, particularly insectivores and nectarivores, broadened in winter when food resources were limited. However, there was niche contraction in several bird species in summer when resources were more readily available. Overall, the forest acted as a refuge for guilds, particularly frugivores and nectarivores, in winter. Furthermore, this study suggested that food limitation is species-specific and does not apply to all species. Understanding the drivers of community change has important implications for forest management and conservation of forest flora and fauna.

For my mom, Sandy Shunn

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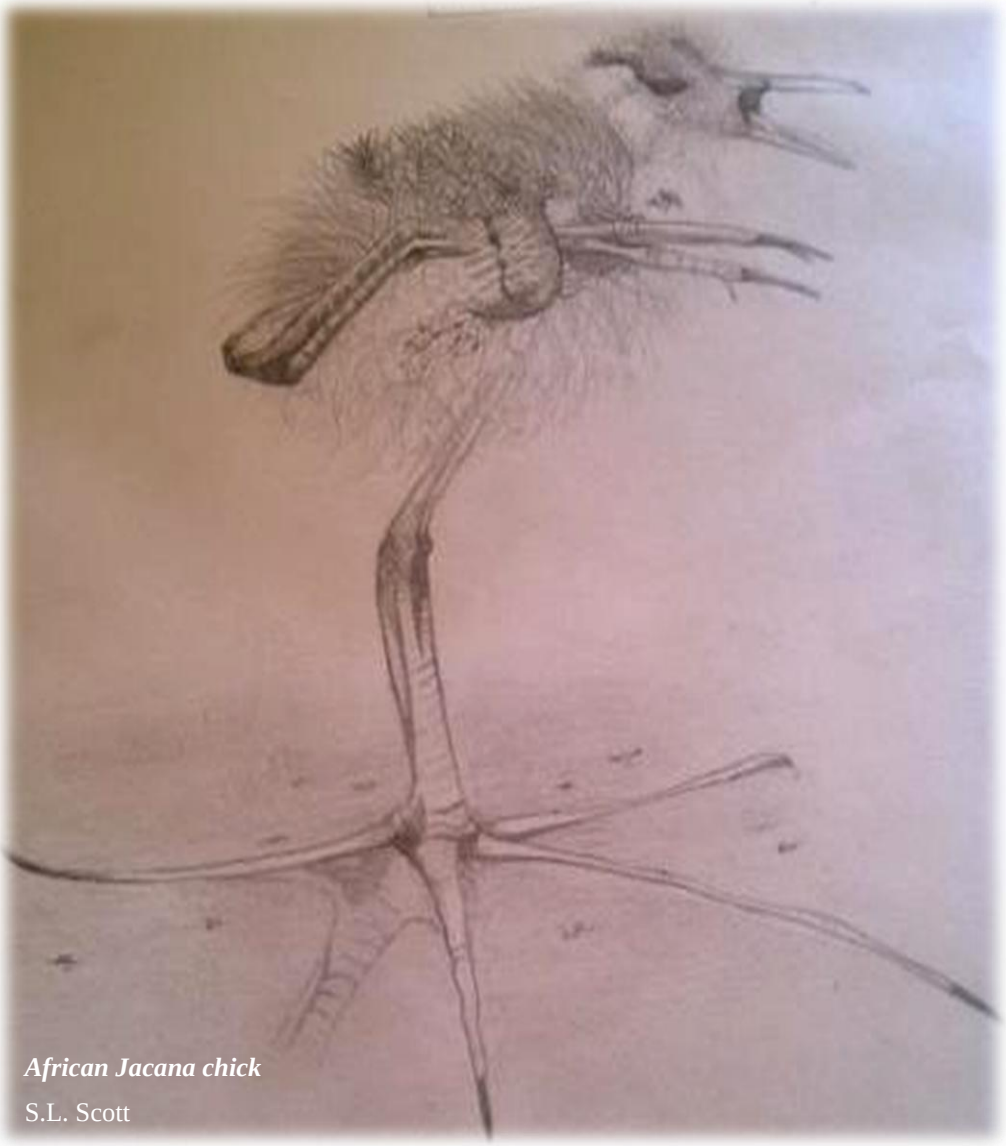
Shine on you crazy diamonds.



African Jacana chick
S.L. Scott

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Preface

Indigenous forest is the smallest and most widely dispersed biome in South Africa. It is not continuous but naturally fragmented within a non-forest matrix, often grassland. Most forest fragments are small, with few patches > 1 km^2. However, despite conservation efforts, forests are still under anthropogenic pressure to harvest products, such as wood. Several patches no longer exist due to extensive exploitation in the past. Therefore, conservation and management schemes tend to focus on individual stands, instead of the forest network. Food varies over space and time and is one of the most important limiting resources to terrestrial birds and therefore an important driver of community dynamics. Understanding resource use by forest birds, and the changes in composition and function that occur in a forest bird community due to periodic food abundance, provides insight to forest management. Therefore, the aim of the study was to describe and quantify the available food resources in an indigenous forest patch, and the exploitation of these resources by birds, at both a spatial and temporal level. This was assessed through a combination of field techniques and stable isotope analysis.

There are five chapters in this dissertation including a general introduction, three data chapters (intended for publication), and a discussion and conclusion chapter. Chapter 1 provides a detailed background to South African forests, particularly the Mist Belt Mixed *Podocarpus* forests, part of the Afromontane forest system. A review of bird community and foraging ecology is provided, with a brief introduction to guilds, niche theory, and stable isotope analysis. Each data chapter is structured for the submission to a peer-reviewed journal to facilitate immediate publication. Therefore, each chapter has its own methods, results, and discussion sections with a reference list. Chapters 2 and 3 are co-authored papers by Samantha L. Scott and Craig T. Symes, and chapter 4 is co-authored by Samantha L. Scott, Craig T. Symes, Stephan M. Woodborne, and Andrew E. McKechnie. Chapter 5 presents and discusses the conclusions of the dissertation.

Repetition is inevitable because many concepts are important to the overall study and individual papers. A glossary of terms is at the end of the dissertation. All bird nomenclature follows Hockey *et al.* (2005). Plant and invertebrate collection was under permit (25/05/2010 - 28/02/2011) of Ezemvelo KwaZulu-Natal Wildlife (EKZNW) and animal ethics clearance was obtained from the University of the Witwatersrand prior to fieldwork (2010/37/2a).

Chapter 1: An introduction to forest bird ecology

'Animals are not always struggling for existence, but when they do begin, they spend the greater part of their lives eating' (Elton 1927).

http://www.biodiversityexplorer.org/birds/musophagidae/tauraco_corythaix.htm

1.1. Community ecology

Most animals do not live in isolation but occupy a shared environment within which several species interact in a direct or indirect manner (Perrins and Birkhead 1983; Wiens 1989; Pomeroy and Service 1992). The assemblage of co-occurring species is defined as a community (Wiens 1989). Both evolutionary and ecological processes contribute to community structure where past speciation and extinction events determine the fundamental cohort of species in an area (Wiens 1989). The core of a community is comprised of established species that breed successfully, but is supplemented with, and constrained by, the local movement of various species (Wiens 1989). In addition, some species visit on a regular basis but do not necessarily breed (Wiens 1989). A community is therefore dynamic over space and time because of the movement of species and the periodic influx of visitors (Wiens 1989). The distribution, composition, abundance, morphological, and behavioural attributes of the species involved, and their relationship to the environment, influence community patterns (Wiens 1989). Birds are highly mobile and therefore particularly interesting to study in community ecology. In addition, birds are relatively easy to identify compared to other taxa because of their conspicuous nature. Bird community ecology is concerned primarily with the identification and understanding of patterns and the drivers that characterise the natural assemblage of species (Wiens 1989). How we understand these processes may be important in how we ultimately manage and conserve an environment.

Defined measurements are needed to interpret community organisation (Holmes *et al.* 1979). Field measurements are commonly used to assess the foraging ecology of birds (e.g. Holmes *et al.* 1979; Robinson and Holmes 1984; Holmes and Recher 1986). More recently, stable isotope analysis has become an increasingly popular tool in ecological studies (Bearhop *et al.* 2002; Inger and Bearhop 2008; Symes and Woodborne 2009; Newsome *et al.* 2012). Both methods provide insight into the community structure and dynamics of birds and are discussed in detail.

1.1.1. Community function and the guild concept

Although species richness and abundance measures are widely used to compare the assemblage of different communities (Remsen 1994), the interactions and functional relationships between species are often more important (Wiens 1989). This is because phylogenetically similar species do not always compete for resources, but ecologically similar species do (Simberloff and Dayan 1991; Wilson 1999). Species that have a common

ecology and exploit the same category of resource in a similar manner belong to the same guild (Root 1967; Simberloff and Dayan 1991; Wilson 1999). Guild allocation puts emphasis on the functional component of a community rather than composition, and allows for comparative work between species that are functionally different and between competitor species in an ecosystem (Root 1967; Simberloff and Dayan 1991; Wilson 1999). Guilds, therefore, provide insight into the ecology of species (Root 1967; Mac Nally 1994) and are particularly useful in studies, such as this one that assess specific ecological drivers of community change.

1.1.2. The ecological niche

Species are only able to exploit a portion of environmental variables provided in an ecosystem (Root 1967) through evolution of adaptive traits to exploit particular resources (Perrins and Birkhead 1983). Adaptive traits differ between species and therefore phenotypically different species do not exploit resources in the same way (MacArthur and Pianka 1966; Schoener 1974). The ecological niche is the set of environmental conditions in which a species can exist in a biotic environment (Elton 1927; Hutchinson 1957; Root 1967). A niche has several dimensions in relation to a species' requirements to exploit a resource in the presence of a competitor (Elton 1927; Hutchinson 1957; Root 1967; Wiens 1989). 'Complete competitors' cannot co-exist (Hardin 1960). Therefore, ecologically similar species differ in niche size, shape, location, or overlap (niche similarity), which generally occurs in response to competitive pressure (Hutchinson 1957; Wiens 1989). Intra-guild species overlap considerably in niche requirements (Simberloff and Dayan 1991) but can coexist because they differ in patch use including food selection, forage height, forage range (vertical distribution), or forage substrate (Perrins and Birkhead 1983; Walther 2002).

Niche similarity is not constant because environmental conditions and resource availability fluctuates over time, but because there are several dimensions to a niche, there may be high overlap in one dimension but not in another (Wiens 1989). Any species that cannot compete successfully for a resource is extirpated from the area, as explained by the "Gause Principle" or "Competitive Exclusion Principle" (Gause 1934; Hardin 1960). The position of each species along a set of axes in ecological niche space is fundamental to community structure (Miles and Ricklefs 1984). Therefore, niche identification is a useful tool to compare the organisation of potentially different communities, particularly under changing conditions (Elton 1927; Root 1967).

1.1.3. Food as a limiting resource to birds

Food is one of the most important limiting resources to terrestrial animals (Elton 1927; Fogden 1972; Koen 1992; Pomeroy and Service 1992; Newton 2003). Food-limitation or food-shortage of a species may refer to food-type, availability, quantity, or nutrient status over space and time (Root 1967; Schoener 1974; Wiens 1989; Fleming 1992; Newton 2003), which influences species distribution (Blake 1983; Koen 1992). Co-existing species compete for similar resources and so the interactions between species in a community are largely driven by their relationship to food (Elton 1927; Lack 1968; Wiens 1989; Simberloff and Dayan 1991). Inter-specific competition is reduced or avoided through various mechanisms (Simberloff and Dayan 1991). For example, species differ in food selection, daily foraging times, or vertical distribution (Schoener 1974; Koen 1988; Simberloff and Dayan 1991). The division of food resources between co-existing species is termed resource partitioning (Schoener 1974), and is a contributing factor to community structure (Schoener 1982; Koen 1988).

Most terrestrial ecosystems undergo seasonal or yearly changes in vegetation structure and food availability, which drives bird community dynamics (Root 1967; Wiens 1989; Symes *et al.* 2002). Fruits and flowers, for example, are often conspicuous but production varies on both a seasonal and yearly basis, and they are therefore considered to be patchy and ephemeral (Fogden 1972; Karr 1976; Fleming 1992; Newton 2003; Borghesio and Laiolo 2004). Birds inhabiting areas in which food is periodically available must possess adaptations to cope with a variable food supply (Root 1967; Fleming 1992). In the short-term, birds either restrict breeding periods to different parts of the year or perform short- (local or altitudinal), or long-range (latitudinal) migratory movements to areas where food resources are relatively abundant (Karr 1976; Koen 1992; Fleming 1992; Poulin *et al.* 1994; Newton 2003; Borghesio and Laiolo 2004). Some species seasonally shift their diet altogether to feed on a different set of resources (Karr 1976; Koen 1992; Newton 2003; Borghesio and Laiolo 2004). This is known as diet-switching (Koen 1992; Newton 2003).

Bird foraging or feeding ecology is an important part of bird community ecology, as the methods in which food is obtained determines the relative success of competing species (Perrins and Birkhead 1983; Robinson and Holmes 1984). Food utilization patterns of birds provide insight into the factors determining bird community organisation and guild structure (Holmes and Recher 1986; Borghesio and Laiolo 2004).

1.2. Forest

Forests are distinct ecosystems with a complex multilayered vegetation structure, and provide a diverse range of food resources that support unique faunal communities (Hopkins 1977; Pomeroy and Service 1992; Castley and Kerley 1996; von Maltitz *et al.* 2002; Hemp 2005; Mucina and Geldenhuys 2006). The forest canopy layer is generally continuous and there is no substantial grass layer on the ground, although shade-tolerant grass species do exist (Pomeroy and Service 1992). Forests have a greater productivity relative to semi-arid and arid environments (Opdam and Wiens 2002). Species richness is high in forests because of the high number of vertical layers, and the addition of major supporting structures, such as boles and branches in the higher strata (MacArthur and MacArthur 1961, Robinson and Holmes 1984; Pomeroy and Service 1992). The vertical layers in a forest provide a variety of foraging opportunities for guilds that are morphologically adapted to manoeuvre through the forest and for locating and exploiting prey on substrates, such as bark, twigs, leaves, and the ground (Holmes *et al.* 1979; Robinson and Holmes 1984; Symes *et al.* 2002). The distribution and variety of food and foraging substrates vary between plant species (Holmes *et al.* 1979), therefore, forest composition and structure influences bird diversity in a forest (MacArthur and MacArthur 1961; Holmes 1986; Borghesio and Laiolo 2004). Forests in southern Africa are similar to tropical forests in fruiting and flowering phenology (Liversidge 1972; Koen 1992; Wirminghaus *et al.* 2001; Herrera *et al.* 2005) but differ structurally, particularly in terms of tree height and patch size.

1.2.1. South African forest: Islands of diversity

South Africa is 1.22 million km^2 of which approximately 5,000 km^2 is indigenous forest (Symes *et al.* 2002; Midgley *et al.* 2003). The forest biome is the smallest (< 1% of land surface) and most widely dispersed biome in the country (Geldenhuys and MacDevette 1989; Midgley *et al.* 2003; Mucina and Geldenhuys 2006; Figure 1). The fragmentation of sub-tropical forest in a non-forest matrix is natural as opposed to temperate and tropical forests, which have suffered fragmentation due to anthropogenic activities (White 1981; Geldenhuys and MacDevette 1989; von Maltitz *et al.* 2002; Downs and Symes 2004; Mucina and Geldenhuys 2006). Edge effects are pronounced in South Africa compared to the equatorial forests of Africa, due to the small size of forest patches (Oatley 1989; Eeley *et al.* 1999; Eeley *et al.* 2001). Despite the small area of land covered by the forest biome, patches support a great diversity of flora and fauna, particularly birds and mammals (Castley and Kerley 1996; Eeley *et al.* 1999; Symes and

Woodborne 2009). In addition, the forest biome holds the highest proportion of biome-restricted species in South Africa of which several are endangered (Castley and Kerley 1996). Fragmented forests are particularly important to study in terms of bird community changes because they are essentially 'islands' within a matrix that is structurally and functionally different (White 1981; Cody 1983; Opdam and Wiens 2002).

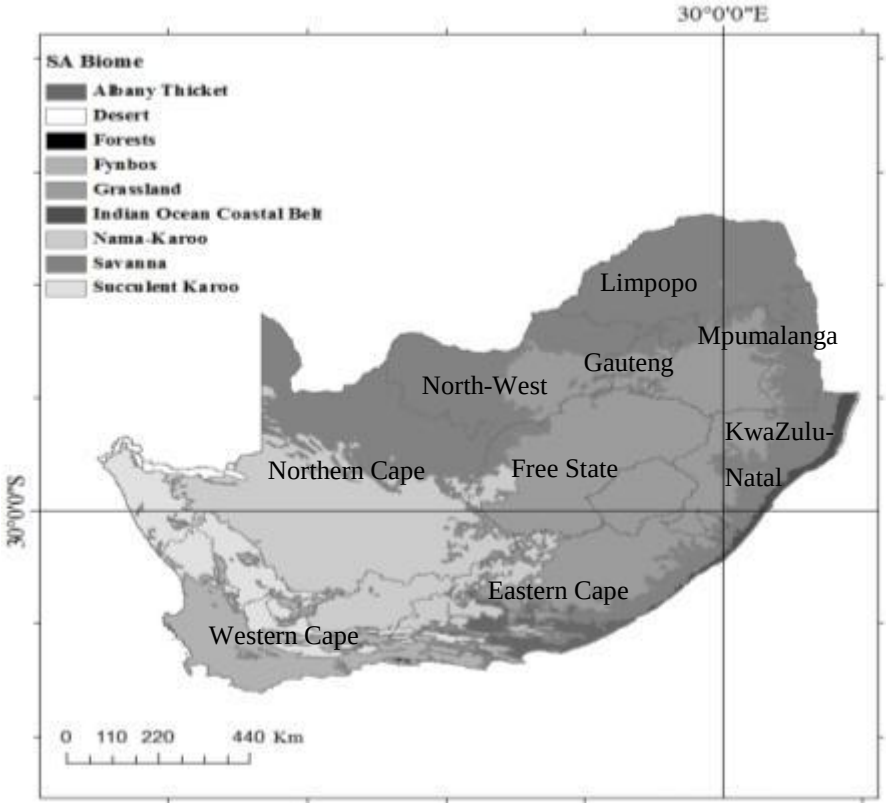

Figure 1. Provincial map of South Africa illustrating the major biomes.

The three broad classifications of forest in South Africa are Afromontane, Scarp, and coastal Lowland forest (Eeley *et al.* 1999), of which Afromontane Forest comprises the largest proportion (Low and Rebelo 1996). KwaZulu-Natal supports all three forest-types and is therefore important in the conservation efforts of forest floral and faunal diversity in South Africa (Eeley *et al.* 1999; Eeley *et al.* 2001; Midgley *et al.* 2003). Afromontane forest patches in KwaZulu-Natal are restricted to the south and southeast slopes of the Great Escarpment where regular fire in the surrounding montane grassland maintain the forest-grassland ecotone (Kotze and Samways 2001; Midgley *et al.* 2003; Mucina and Geldenhuys 2006; Bond and Parr 2010; Figure 2).

Afromontane Forest comprises two forest sub-types, Montane *Podocarpus* Forest and Mist Belt Mixed *Podocarpus* Forest (Eeley *et al.* 1999; Midgley *et al.* 2003). The Mist Belt

Forest group comprises the Northern Mist Belt Forests of the Limpopo and Mpumalanga Provinces and the Southern Mist Belt Forests of the Eastern Cape and KwaZulu-Natal (Mucina and Geldenhuys 2006). Forest patches vary in size [< 0.001 - 992 ha; mean ± SD = 24.6 ± 70.9; n = 1743; *Source:* Department of Agriculture, Fisheries and Forestry (DAFF)] but large forests (> 200 ha) are scarce and only a few can be recognised in the country today, for example the Ngome, Qudeni, and Nkandhla forests in KwaZulu-Natal (Oatley 1984; Eeley *et al.* 1999; Mucina and Geldenhuys 2006).

Figure 2. Afromontane forest distributed within a grassland matrix along the south and southeast facing slopes of KwaZulu-Natal. Several forest fragments are visible in the background.

Patch-use by birds may differ due to differences in latitude, altitude, and the local environment, such as climate, fire, gap dynamics, and anthropogenic influences on forests (Hawkins 1999; Opdam and Wiens 2002; Sharam *et al.* 2009; Bond and Parr 2010). The number, quality, size, and distance between suitable forest patches together with matrix characteristics have an influence on bird community diversity, dynamics, and distribution in the landscape (Poulin *et al.* 1994; Opdam and Wiens 2002; Newton 2003; Watson *et al.* 2004). Smaller isolated forest patches (≤ 50 ha) are important components of the forest biome and form a fragmented network within the system (Mucina and Geldenhuys 2006; Figure 2).

The process of natural forest fragmentation occurs over a long time, removing the already small fragments and reducing the size of the remaining larger fragments (Newton 2003). However, anthropogenic activities have contributed to the fragmentation and isolation of forest patches, where large areas of forest have been removed, especially in the eastern regions

of South Africa (Eeley *et al.* 1999; Kotze and Samways 1999; Lawes and Eeley 2000; Opdam and Wiens 2002; Newton 2003). Anthropogenic disturbance affects the composition of bird communities because habitat-suitability may change for some species that may no longer be able to persist in the environment (Wiens 1989; Opdam and Wiens 2002). Commercial activities, such as deforestation, afforestation, overgrazing, fire, or agriculture have altered, and in some cases, completely modified the non-forest matrix (Oatley 1984; Eeley *et al.* 1999; Kotze and Samways 1999; Lawes and Eeley 2000; Wethered and Lawes 2003). Anthropogenic pressure is a global threat to forests not only South African forests (Bennun *et al.* 1996).

Forest conservation has been a priority, mostly of larger patches, on public and private property (Geldenhuys and MacDevette 1989; Kotze and Samways 1999), but is difficult because of the fragmented and isolated nature of forest and because the processes that determine bird community structure are poorly understood (Lawes *et al.* 2000).

1.2.2. Study site: New Forest

New Forest is an Afromontane Mist Belt Mixed *Podocarpus* Forest patch 112.3 ha in area (Cooper 1985) on the privately owned New Forest Farm (29°27'53"S 29°52'54"E; *c.* 1,380 - 1,740 m a.s.l.), KwaZulu-Natal, South Africa (Figure 3).

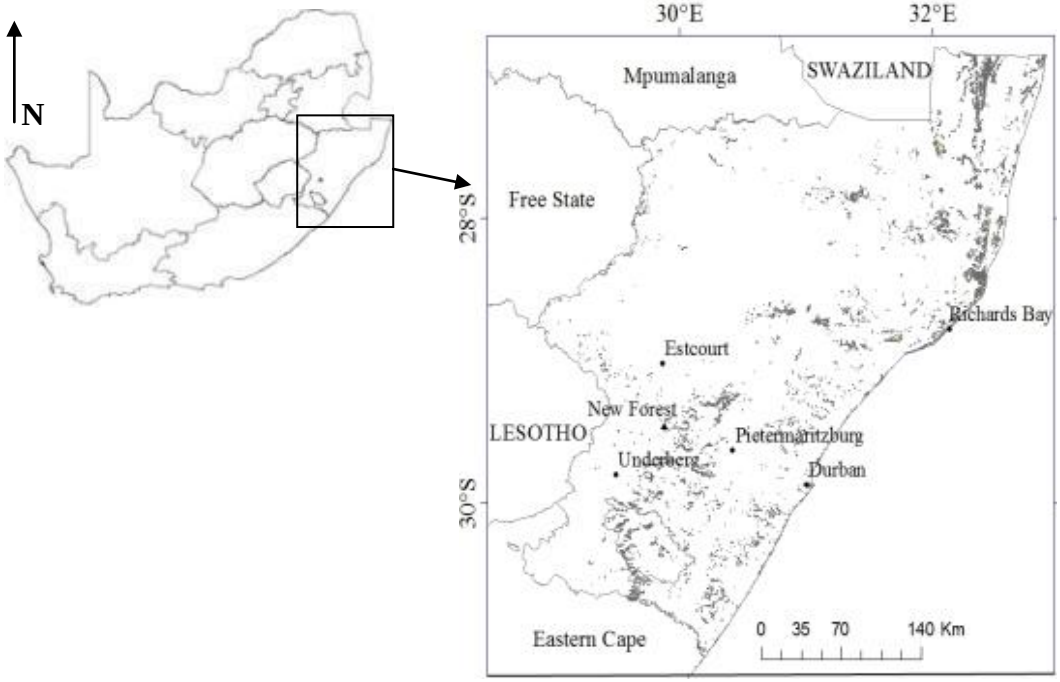

Figure 3. The position of New Forest (triangle) within indigenous forest (grey shading) in KwaZulu-Natal, South Africa [*Source:* Department of Agriculture, Fisheries and Forestry (DAFF)]. Selected towns (dots), neighbouring provinces, and countries (uppercase) are for reference purposes. Inset: The location of KwaZulu-Natal in South Africa.

New Forest is an indigenous forest patch surrounded by montane grassland that is interspersed with exotic plantations (Low and Rebelo 1996; Downs and Symes 2004; Mucina and Geldenhuys 2006; Figure 4). It has a high density of tall evergreen and deciduous trees (*c.* 15 - 20 m) trees, and is multilayered with a dense understory and a well-developed herbaceous layer on the forest floor (Downs and Symes 2004; Mucina and Geldenhuys 2006; Figure 4). Shade-tolerant annuals and several fern species, such as maidenhair, grow on the forest floor (SLS *pers. obs.*). Several lianes and climbers grow in or near the forest openings and toward the forest edge (SLS *pers. obs.*). There are several natural openings in the forest in which a dense layer of wetland plants, such as *Cyperus* (Cyperaceae) and *Kniphofia* (Asphodelaceae) grow, and are enclosed by stands of *Leucosidea sericea* (Rosaceae) (SLS *pers. obs.*). The Umgeni Vlei, the source of the Umgeni River, forms part of a nature reserve at the crest of the mountain and belongs to Ezemvelo KwaZulu-Natal Wildlife (EKZNW). The perennial Umgeni River borders the base of the forest and joins with several gullies that dissect the forest (Figure 4).

Common plants were *Podocarpus latifolius* (Podocarpaceae), *Podocarpus falcatus* (Podocarpaceae), *Celtis africana* (Ulmaceae), *Halleria lucida* (Scrophulariaceae), *Carissa bispinosa* (Apocynaceae), *Eugenia zuluensis* (Myrtaceae), *Gymnosporia harveyana* (Celastraceae), and *Scutia myrtina* (Rhamnaceae) (SLS *pers. obs.*). Invasive plants, especially at the forest edge or forest openings were American Bramble *Rubus cuneifolius* (Rosaceae), *Pyracantha angustifolia* (Rosaceae), and *Solanum* spp. (Solanaceae) (SLS *pers. obs.*). Bramble is invasive in the grassland but attempts have been made to eradicate this species (Kobus Kruger *Pers. Comm.;* Chevonne Reynolds Research Report). In addition to birds, the Chacma Baboon *Papio ursinus* may be responsible for dispersal of Bramble into the forest as they forage in the grassland and often roost in the forest (SLS *pers. obs.*).

This region receives *c.* 1,000 mm of rainfall per annum. Winter (June to August) receives < 50 mm rainfall per month but summer (December to February) receives > 100 mm per month (Mucina and Geldenhuys 2006). Frequent mist supplements rainfall considerably (Figure 4). Mean annual temperature is *c.* 16˚C. Winter temperature ranges from 10 - 20˚C and summer from 18 - 30˚C (Mucina and Geldenhuys 2006).

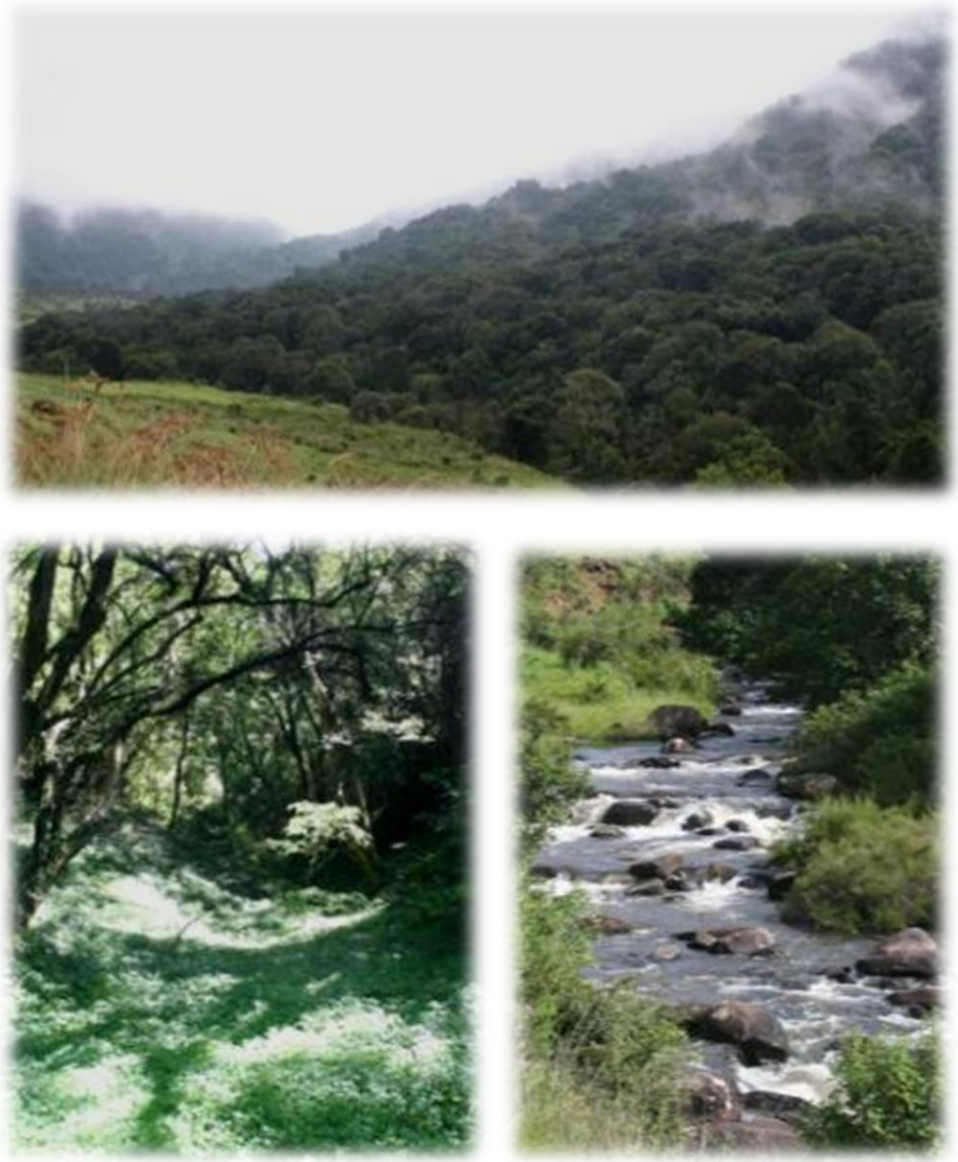

Figure 4. New Forest in a grassland matrix and shrouded in mist, a frequent occurrence in Mist Belt Forest (above). The patch has tall trees and a well-established herbaceous layer (left), and the perennial Umgeni River borders the base of the forest patch (right).

Mammals observed in the forest were the Samango Monkey *Cercopithecus mitis*, Vervet Monkey *Cercopithecus aethiops*, Chacma Baboon, Bushbuck *Tragelaphus scriptus*, Common Duiker *Sylvicapra grimmia*, Bushpig *Potamochoerus larvatus*, and Tree Hyrax *Dendrohyrax arboreus* (SLS *pers. obs.*). Herpetofauna in the forest were Natal Midlands Dwarf Chameleon, *Bradypodion thamnobates* (IUCN: Lower Risk/ Near Threatened), Natal Black Snake *Macrelaps microlepidotus*, Clicking Stream Frog *Strongolopis grayii*, and Guttural Toad *Amietophrynus gutturalis* (SLS *pers. obs.*).

1.2.3. Forest birds

Some birds are highly specialized to the forest environment (Oatley 1989; Bennun *et al.* 1996). These species are known as forest-specific species or forest specialists because they depend on forest for their survival, particularly for breeding purposes (Oatley 1989; Bennun *et al.* 1996). There are 48 forest specialists in South Africa (*c.* 10% of South African terrestrial birds), a disproportionately high number considering that forests occupy < 1% of the country (Midgley *et al.* 2003) and *c.* 5% of KwaZulu-Natal (92,285 km^2; Eeley *et al.* 2001). However, forest dependency varies within and between bird species (Bennun *et al.* 1996; Symes *et al.* 2002; Neuschulz *et al.* 2011). Forest generalists are birds that are partly dependent on forest resources, particularly for breeding purposes, but are commonly recorded at the forest edge or in other wooded environments (Bennun *et al.* 1996, Neuschulz *et al.* 2011). Forest visitors are birds that are commonly recorded in other vegetation-types and not entirely dependent on the forest environment for survival (Bennun *et al.* 1996). Forest specialists, and to some extent forest generalists, are important to identify because they are most likely to disappear when forests are extensively modified or removed (Bennun *et al.* 1996; Neuschulz *et al.* 2011). This is because forest specialists are less widespread than other bird species, are sensitive to disturbance, and are reluctant to cross non-forest gaps between indigenous forest patches (Bennun *et al.* 1996). Therefore, both food availability and suitable habitat affect the distribution of these species (Oatley 1989; Wethered and Lawes 2003).

1.3. Stable isotopes as a tool

Stable isotopes are natural, abundant molecules that form part of all matter (Fry 2006). They are atoms of a given element that have the same number of protons and electrons but differ in the number of neutrons (Inger and Bearhop 2008). Light isotopes of an element are often more abundant than their heavier counterpart (Fry 2006) and the ratio of light to heavy isotopes in an organism's tissues determines its isotopic signature. The signatures vary between organisms and vegetation types and because the tissues of an animal reflect the signature of their diet, information can be gained on foraging preferences, trophic level, and habitat selection of an individual (Inger and Bearhop 2008).

Stable carbon and nitrogen isotopes are valuable non-radioactive tracers in ecological research (Schindler and Lubetkin 2004; Newsome *et al.* 2012), and a dual-isotope approach is useful (Post 2002; Inger and Bearhop 2008). Plants in forests and grasslands generally have different isotopic signatures. This is because the plants use different photosynthetic pathways,

where forests are C_3-dominated (shade-tolerant species) but the surrounding grassland is C_4-dominated (light-dependent species). C_3 plants are depleted in ^{13}C with values of -27 to -29‰ compared to C_4 and CAM plants of *c.* -13‰, which have similar photosynthetic pathways and cannot be distinguished effectively using carbon isotopes (Bird *et al.* 1994; Herrera *et al.* 2003; Symes and Woodborne 2009). The difference between the carbon signatures in each environment means that carbon isotopes can be used to indicate the basal plant sources to consumers, distinguishing the relative contribution of carbon from C_3 or C_4/CAM pathways of plants (Peterson and Fry 1987; Herrera *et al.* 2003).

Nitrogen isotopes, on the other hand, function as trophic level indicators and are used to delineate trophic levels in a forest system (Peterson and Fry 1987; Herrera *et al.* 2003). Trophic structure contributes information about bird community structure and organisation because it reflects, to some degree, the importance of various resources to birds as well as availability (Blake 1983). Carbon and nitrogen isotopes in food webs are particularly useful because there is a predictable relationship between the isotope signature of a consumer's tissue and its diet (Bearhop *et al.* 2002; Schindler and Lubetkin 2004; Symes and Woodborne 2009).

Tissues differ in their turnover rates and therefore contribute short- or long-term information on diet and at different spatial scales for mobile animals, particularly birds (Hobson and Clark 1992a; Bearhop *et al*. 2002; Ogden *et al.* 2004). Blood and faecal matter are considered non-destructive methods to assess the isotopic signatures of birds and are therefore useful when multiple samples are required (Hobson and Clark 1992b; Bearhop *et al.* 2002). Blood primarily reflects dietary protein within the past three weeks of capture (Bearhop *et al.* 2002; Ogden *et al.* 2004) whereas faecal matter reflects intake within the last few hours. Age does not affect the $\delta^{13}C$ and isotopic signatures of tissue or diet-tissue fractionation factors (Hobson and Clark 1992b). However, many other factors influence the isotopic signatures including metabolic processes and nutrient stress among others, which may affect the $\delta^{15}N$ signature of some species more than other species (Hobson and Clark 1992a; Hobson and Clark 1992b; Vanderklift and Ponsard 2003). In addition, there are often seasonal differences in both the quantity and quality (particularly nitrogen) of food resources in the system. Therefore, adequate sampling of the prey and basal food sources becomes important to account for these differences and aid in the interpretation of results (Inger and Bearhop 2008).

It is not completely possible to understand an entire community at an isotopic level (Symes and Woodborne 2009) because there are confounding factors in the dietary analysis

of animals using isotopes. Firstly, the isotope composition of several tissues reflects the particular nutrient components from which they are synthesized and not the bulk diet of the animal (Bearhop *et al*. 2002). Second, in tissues where uncommon or limiting nutrients are required for synthesis, assimilation rates could vary as some of these dietary components are mobilized from long-term stores rather than from the current diet (Bearhop *et al*. 2002). However, stable isotopes are a useful and powerful tool in understanding complex food webs and the feeding biology within bird communities of which little is known, particularly when combined with conventional methods (Inger and Bearhop 2008; Symes and Woodborne 2009). Therefore, stable isotope analysis alone is generally not good enough to solve ecological questions about niche exploitation and differentiation, but should be used in conjunction with other sources of evidence, such as behavioural observations (Fry 2006; Inger and Bearhop 2008).

1.4. Overall aim and objectives

Most bird communities are characterised by the spatio-temporal dynamics in foraging ecology but the effect of seasonality on tropical Africa has not been well studied (Borghesio and Laiolo 2004). Most forest research in South Africa has been conducted in the Eastern Cape, with little work in KwaZulu-Natal and even less in the forests of the Mpumalanga and Limpopo Provinces (Brown 2006). There is also a scarcity in the research of the community structure of forest avifauna in any forest-type in South Africa (Symes *et al.* 2002; Monadjem 2003; Brown 2006), particularly with respect to birds and food availability (Koen 1992).

Southern African forests, like tropical forests, have an irregular and highly variable intra- and inter-seasonal fruiting and flowering phenology (Liversidge 1972; Koen 1992; Wirminghaus *et al.* 2001; Herrera *et al.* 2005). In addition, structural changes occur between seasons because several of the tree species are deciduous (Wirminghaus *et al.* 2001). Therefore, the forest changes both functionally and structurally between seasons. To observe seasonal differences in the community structure and foraging ecology of forest birds, two distinct seasons, winter and summer, were chosen for comparison where food resources and structural attributes of the forest were most likely to be different.

Therefore, the aim of the project was to describe and quantify the available food resources in an indigenous forest and the exploitation of the available resources by birds, at both a spatial and temporal level. The three main objectives of the project were to assess:

1. The change in compositional (richness and abundance) and functional (feeding guilds) diversity of a forest bird community between winter and summer;
2. Niche separation and resource partitioning of forest birds with respect to seasonal changes in vegetation structure and food availability through behavioural and stable isotope analysis;
3. The overall importance of indigenous forest to birds and the implications for conservation.

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Chapter 2: Food drives changes in a bird community

Seasonal variation in food availability drives bird community changes in a forest patch

Samantha L. Scott* and Craig T. Symes

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, P/Bag 3, Wits 2050, South Africa

* Corresponding author

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***Corresponding author:**

Samantha L. Scott

School of Animal, Plant and Environmental Sciences

University of the Witwatersrand

Private Bag 3

Wits, 2050

South Africa

Email: samalamanam@gmail.com

Telephone: +27 (0)11 717-6478

Facsimile: +27 (0)11 717-6494

2.1. Abstract

Seasonal changes in the composition and function of an Afromontane Forest bird community, in response to changes in food availability between winter (dry season) and summer (wet season), were assessed. Point counts were used to assess bird richness and abundance. Flower and fruit density and abundance and invertebrate abundance were recorded in 400 m^2 quadrats. Bird diversity and richness were significantly higher in summer than winter. Many birds were forest generalists and forest visitors; however, the greatest richness and abundance of birds in both seasons remained forest specialists. The greatest abundance and biomass of birds in winter were nectarivores, granivores, and frugivores, but insectivores and omnivores were significantly greater in summer. This pattern was due to the mass flower and fruit contribution by conspicuous canopy tree species, *Halleria lucida* and *Podocarpus latifolius* in winter, and an increase in invertebrate diversity in summer. Invertebrate diversity together with an increase in fruit abundance in the understory provided a greater food variety and abundance to omnivores in summer. This study demonstrated that changes in the composition and function of a forest bird community are driven by seasonal food availability and the forest is an important refuge to birds in winter, particularly nectarivores and frugivores.

Keywords: Afromontane Forest, community dynamics, compositional changes, functional turnover, food availability

2.2. Introduction

Food availability fluctuates through space and time (Fleming 1992; Wirminghaus *et al.* 2001; Newton 2003) and is an important resource to terrestrial birds (Lack 1968; Holmes *et al.* 1979; Holmes and Recher 1986; Koen 1992; Symes *et al.* 2002). Forests have a complex multilayered vegetation structure and provide a diverse range of food resources that support unique bird communities (Hopkins 1977; Castley and Kerley 1996; von Maltitz *et al.* 2002; Hemp 2005; Mucina and Geldenhuys 2006). Fruit and flowers are often conspicuous and easily located in forests but availability is patchy and ephemeral over space and time, which favours highly mobile taxa, such as birds, which operate on large spatial scales in search of food (Fleming 1992; Newton 2003; Herrera *et al.* 2005). Birds respond to food-limitation of patchily distributed resources through diet-switching or performing short- or long-range movements from areas where food is scarce to areas where food is relatively more abundant

(Fleming 1992; Koen 1992; Poulin *et al.* 1994; Wirminghaus *et al.* 2001; Newton 2003; Symes and Marsden 2007). Seasonal movements of varying spatial magnitudes are common in fruit- and nectar-feeding birds (e.g. Fleming 1992; Kimura *et al.* 2001; Cotton 2007). Food limitation has an important influence on the life history strategies of birds in a community including movement patterns, breeding biology, and social interactions (Lack 1968; Fleming 1992; Koen 1992; Newton 2003). Food availability, therefore, influences the composition and function of a bird community over time.

The sub-tropical forests of southern Africa are similar to tropical forests in that there is an irregular and highly variable intra- and inter-seasonal fruiting and flowering phenology (Liversidge 1972; Koen 1992; Wirminghaus *et al.* 2001). However, southern African forests are not continuous, but naturally fragmented in a surrounding matrix (White 1981; von Maltitz *et al.* 2002; Mucina and Geldenhuys 2006). In addition, anthropogenic activities, such as deforestation have contributed to the fragmentation and isolation of forest patches (Eeley *et al.* 1999; Kotze and Samways 1999; Lawes and Eeley 2000). In South Africa, indigenous forest is the smallest (< 1% of land surface) and most widely dispersed biome in the country (Geldenhuys and Knight 1989; Mucina and Geldenhuys 2006). Despite the small area of land covered, indigenous forest supports a great diversity of avifauna, approximately 14% of the terrestrial birds in southern Africa (Geldenhuys and MacDevette 1989; Eeley *et al.* 2001).

Some forest birds are more dependent on the forest environment that other species (Symes *et al.* 2002). Forest-specific species or forest specialists, for example, are completely dependent on forest resources for reproduction and survival (Oatley 1989; Bennun *et al.* 1996). In addition, these species are reluctant to move across large gaps between forest patches and therefore food becomes an important limiting resource (Oatley 1989; Wethered and Lawes 2003). There are 48 described forest-specific species (*c.* 10% of South African terrestrial birds), a disproportionately high number considering that forests occupy a small portion of South Africa, and *c.* 5% of KwaZulu-Natal (92,285 km^2; Eeley *et al.* 2001). Some forest birds, however, are only partly dependent on forest resources and are commonly recorded at the forest edge or other wooded environments. These species are termed forest generalist or forest-associated species (Bennun *et al.* 1996; Lawes *et al.* 2000; Neuschulz *et al.* 2011). Bird species not dependent on the forest environment and most commonly recorded in other vegetation-types are termed forest visitors (Bennun *et al.* 1996). In general, forest specialists are less widespread than other forest birds (Bennun *et al.* 1996). Forest specialists, and to some extent generalists, are important to identify, as they are most likely to

disappear in extensively modified forest (Bennun *et al.* 1996), and are therefore of greater conservation concern.

Research in African forest has focused on several aspects of bird community ecology, particularly of the biogeography of forest birds (e.g. Burgess and Mlingwa 1993; Reif *et al.* 2006; Munyekenye *et al.* 2008). In addition, descriptive work on the community composition, structure, distribution, and diversity of forest birds and the importance of forested areas to birds (and the conservation value of forest bird species) is extensive (e.g. Cody 1983; Burgess *et al.* 1998; Dinesen 1998; Hawkins 1999; Nuttall and Parker 2001; Symes *et al.* 2002; Monadjem 2003; Burgess *et al.* 2007). Research has also highlighted the influence of structural effects, such as edge or matrix effects, on forest bird communities (e.g. Krüger and Lawes 1997; Wethered and Lawes 2005) and the effect of forest destruction on forest bird conservation (e.g. Dunn 2004; Spottiswoode *et al.* 2008; Neuschulz *et al.* 2011). However, research has not sufficienty addressed the seasonal turnover in composition and function of a forest bird community in response to seasonal food availability in a forest patch. Understanding the main drivers of change in a forest bird community has important implications for forest bird conservation, especially in terms of function. Therefore, the aim of the study was to assess the seasonal changes in an Afromontane Mist Belt Mixed *Podocarpus* Forest bird community in response to changes in food availability between winter and summer. The following questions were addressed; was there 1) a change in forest bird diversity and composition between seasons, 2) functional turnover in the forest bird community between seasons and, 3) a corresponding change in food availability between seasons?

2.3. Methods

2.3.1. Site description

Data were collected during winter (15 July to 22 August 2010) and summer (16 January to 26 February 2011) in a forest patch on the privately owned New Forest Farm (29°27'53"S 29°52'54"E; *c.* 1,380 - 1,740 m a.s.l.), KwaZulu-Natal, in South Africa (Figure 1). New Forest is an Afromontane Mist Belt Mixed *Podocarpus* Forest patch 112.3 ha in area (Cooper 1985). The patch is situated within a grassland matrix, interspersed with exotic plantations, on the south and southeast facing slopes (Low and Rebelo 1996; Downs and Symes 2004; Mucina and Geldenhuys 2006). It has a high density of tall evergreen and deciduous trees (*c.* 15 - 20 m) trees, and is multilayered with a dense understory and a well-developed herbaceous layer on the forest floor (Downs and Symes 2004; Mucina and Geldenhuys 2006).

There are several natural openings in the forest in which a dense layer of wetland plants, such as *Cyperus* and *Kniphofia* spp. grow, and are enclosed by stands of *Leucosidea sericea*. The Umgeni Vlei, the source of the Umgeni River, forms part of a nature reserve at the crest of the mountain and belongs to Ezemvelo KwaZulu-Natal Wildlife (EKZNW). The Umgeni River borders the forest to the south and joins with several gullies that dissect the forest.

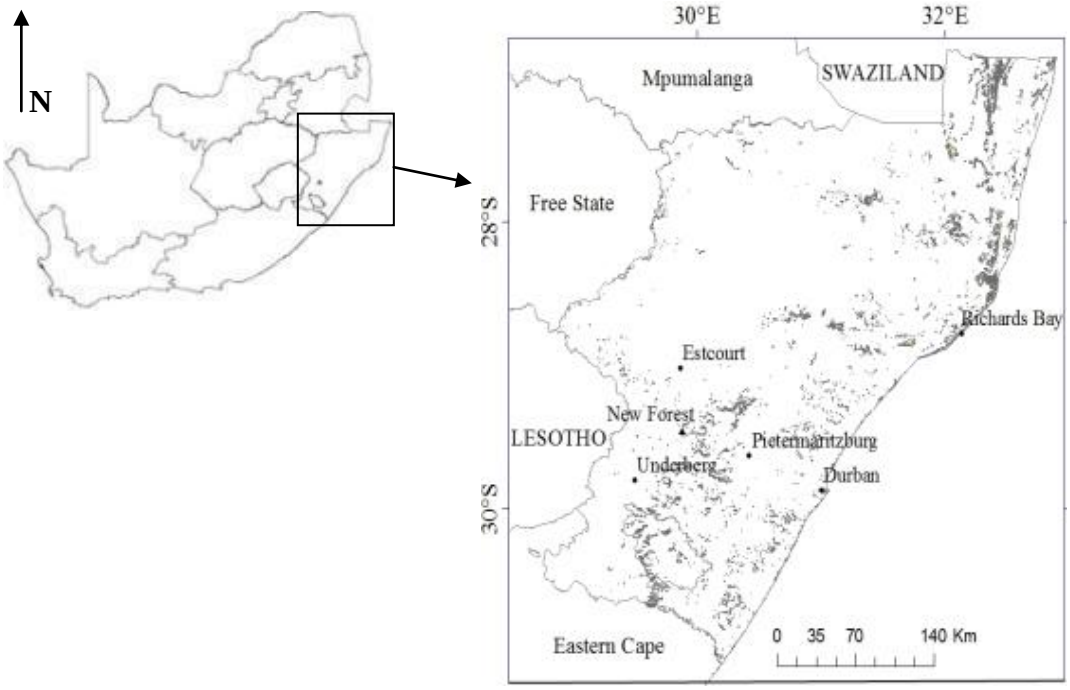

Figure 1. The position of New Forest (triangle) within indigenous forest (grey shading) in KwaZulu-Natal, South Africa [*Source*: Department of Agriculture, Fisheries and Forestry (DAFF) in South Africa]. Selected towns (dots), neighbouring provinces, and countries (uppercase) are for reference purposes. Inset: The location of KwaZulu-Natal in South Africa.

Precipitation in the Southern Mist Belt Forest regions is *c.* 1,000 mm per annum with a distinct wet and dry season; winter (June to August) receives < 50 mm rainfall per month whilst summer (December to February) receives > 100 mm per month, with frequent mist which supplements rainfall considerably (Mucina and Geldenhuys 2006). The mean annual temperature is *c.* 16˚C where winter temperatures range from 10 - 20˚C and summer temperatures from 18 - 30˚C (Mucina and Geldenhuys 2006).

2.3.2. Bird sampling

Forest avifauna was censused using the point-count method (Reynolds *et al.* 1980). A total of 57 point counts were sampled in winter and re-sampled in summer over each sampling

period. Sampling took place on clear days throughout the study period. Although the majority (74%) of point counts were conducted from 05h00-11h00, sampling took place throughout the day because daily bird activity is variable (Skead 1964). Random point-counts (25 m radius) were at least 60 m apart where all individuals were identified audio-visually during a 10 min period (Krüger and Lawes 1997; Manu and Cresswell 2007). The observation period began while walking slowly to the centre point where the observer (SLS) waited quietly for birds (Skead 1964; Koen and Crowe 1987; Koen 1988a). The time was sufficient to record cryptic species but short enough to reduce potential pseudo-replication (Krüger and Lawes 1997). As some forest species flush easily, a supplementary band from 25-50 m was sampled to record additional species beyond the 25 m radius. Birds circling low above the forest canopy were recorded as they may have been using the forest to search for prey, however any bird passing through or high above the point count was not recorded, as they were less likely to be utilising the forest. Lastly, bird species seen or heard between sampling sessions were recorded to provide a comprehensive species list of the forest. A Global Positioning System (GPS) receiver was used to record the centre of each point for re-sampling in summer, and to measure the distance between points. Preliminary surveys conducted prior to data collection were to ensure accurate bird identification.

2.3.3. Flower and fruit production

Food in the form of nectar (estimated as flower abundance, and hereafter termed 'flowers'), and whole fruit was quantified in 12 quadrats of 20 x 20 m (400 m^2) distributed throughout the forest (modified from Krüger and Lawes 1997). Sampling was done once per quadrat per season. Each quadrat was selected on the homogeneity of slope, aspect, and vegetation. The GPS details were recorded at the centre and flagging tape placed at the corners of each quadrat for re-sampling in summer.

It was difficult to count the number of flowers and fruit (crop) produced per tree accurately. Therefore, crop abundance was estimated according to defined categories: 0 - 10, 10 - 100, 100 - 1,000, and 1,000 - 10,000. Tree height (m) was estimated using a metre rule for reference as a clinometer proved unreliable where vegetation was dense. Trees with at least half of their trunks within the quadrat were considered. Plant specimens were collected for identification to species and for reference purposes.

2.3.4. Invertebrate sampling

Invertebrate sampling occurred over three days within six quadrats per season. Five pitfall traps, (white plastic cups 108 x 60 mm), were buried flush with the ground surface and ≥ 5 m apart per quadrat (n = 30 per season). Each trap was subsequently filled with a non-toxic surfactant solution (1 drop dishwashing liquid per 1 L tap water) to ensure the entrapment of invertebrates. In addition, commercially available 90 x 150 mm AgriBiol® 'bug traps' (Vlaeberg, South Africa), coated with a non-toxic glue, were used to collect invertebrates in the forest understory. Two traps (one blue and one yellow) were fastened with rope to a tree trunk or branch facing north at both 1 m and 3 m above the ground respectively. Four traps were assigned to each quadrat totalling 24 sticky traps per season. Sweep netting was done for five minutes per day (an average of 30 - 50 sweeps per minute depending on the openness of vegetation) within the lower 2 m of the forest, which was enough time to sample the entire quadrat. The traps were checked every morning and invertebrates removed and stored in 75% alcohol for later identification to morphospecies. All capture methods, although in the lower strata, were used to assess seasonal changes in invertebrate availability. The traps were removed at the end of winter and replaced in summer, as required by the landowner.

2.3.5. Data analysis

Data were tested for normality prior to all statistical analyses and all statistical analyses were conducted in Statistica 6.1.478.0 (Statsoft. Inc. 2004), unless otherwise stated. Bird nomenclature follows Hockey *et al.* (2005). Birds were categorized as forest specialists (Oatley 1989), forest generalists, and forest visitors (Bennun *et al.* 1996), according to the definitions given above. Bird abundance was analysed only from data collected within the 25 m radius to reduce the effect of pseudo-replication and overestimation of the number of individuals. A bird species list of the forest, together with the abundance, and relative abundance (RA) of birds where applicable, was generated. A Wilcoxon Sign Test was used to test for significant changes in species abundance between seasons. Relative abundance (RA) was calculated based on the equation:

$$RA\ (\%) = (Species\ abundance/Total\ bird\ abundance\ per\ season) \times 100 \quad (1)$$

All calculations involving incidence data were analysed from the 50 m radius because an additional 10 bird species were recorded in the 25 - 50 m band during the point counts,

and these data contribute to the overall understanding of compositional changes in the bird community. Incidence data record a change in richness only; therefore, the effect of pseudoreplication is negligible. The Incidence-Based Estimator (ICE) was used to estimate actual species richness (Colwell 2006). A Paired T-test was used to test for a significant difference in species richness and a Wilcoxon Sign Test was to test for differences between Shannon-Wiener diversity. Sampling completeness was calculated from the Chao2 estimator as the percentage of species estimated to occur in the sampling pool that were observed during sampling sessions (Sobéron *et al.* 2007; also see Masterson *et al.* 2009).

Bird species were categorized into feeding guilds based on published dietary information (Hockey *et al.* 2005). Many non-insectivorous bird guilds occasionally feed on insects (Fleming 1992) and so the dominant dietary component was used to determine a species feeding guild. A Wilcoxon Sign Test was used to test for significant seasonal changes in, 1) the abundance of intra-guild species and, 2) the bird biomass ($g.ha^{-1}$) in the forest. Biomass was calculated based on the mean mass (g) of each species, and where applicable, the average values of male and female mass (Hockey *et al.* 2005). The proportional biomass (%) of each feeding guild was calculated from the total biomass (g) for each season:

$$\textit{Proportional biomass (\%)} = \textit{[Guild biomass (g)/Season total biomass (g)]} \times 100 \qquad (2)$$

Crop production per tree was recorded in defined categories, where the upper value represented the potential maximum crop abundance that a particular tree could produce. The upper value per category per plant species was therefore used for all further analyses. Crop density was calculated as:

$$\textit{Crop density (crop abundance/m}^2\textit{)} = \textit{Total crop produced/Quadrat area (m}^2\textit{)} \qquad (3)$$

Where total crop produced was the combined crop abundance produced by all trees providing the same resource, fruit or flowers within a quadrat, regardless of species. These data were compared between seasons using a Wilcoxon Sign Test. Overall availability is a measure of productivity in the forest, therefore, all flowers and fruit abundance measures were combined within their respective categories and analysed. Thereafter, food resources likely to attract bird species were then compared between seasons. The RA was calculated using equation (1).

For invertebrate availability, Shannon-Weiner diversity, Abundance-Based Estimator (ACE) and Chao1 estimator of species richness were calculated from pooled morphospecies

and abundance values in EstimateS 7.5.2 (Colwell 2006), and compared using an Independent T-test.

2.4. Results

2.4.1. Bird diversity

Bird diversity was significantly higher in summer than winter, even with the exclusion of migrant species (Wilcoxon Sign Test; $Z = 6.6$; $p < 0.05$; Table 1). Bird species richness and abundance were slightly higher in summer than winter, although the difference in abundance was insignificant (Paired T-test; $t = 1.76$; $p = 0.08$; Table 1). In both seasons, forest specialists accounted for > 50% of the individuals, and together with generalists accounted for > 70% (Table 1). Summer had a significantly higher abundance of forest visitors than winter (Wilcoxon Sign Test; $Z = 3.2$; $p < 0.05$; Table 1).

Table 1. Bird diversity in New Forest using abundance values (25 m radius).

Season	Shannon -Wiener	Richness	Significant increase	Abundance	Forest specialist	Forest generalist	Forest visitor
Winter	2.7	29	3 (8)	352	196 (15)	98 (7)	58 (7)
Summer	2.9	35	8 (20)	442	244 (17)	78 (9)	120 (9)
Migrants excluded	2.8	33	7 (21)	435	243 (16)	78 (18)	114 (8)

[1]Shannon-Wiener diversity, species richness, and abundance of forest birds between winter and summer. The number and proportion (%) of species that increased significantly in abundance, and the abundance and richness of forest specialists, generalists, and visitors are indicated.

At species-level, 11 bird species (27.5%) increased significantly in abundance in either winter or summer. Three species increased significantly in abundance in winter and eight species increased significantly in summer (Table 1). Southern Double-collared Sunbird *Cinnyris chalybeus* (22.7%) and Dark-capped Bulbul *Pycnonotus tricolor* (10.8%) were two of the three most abundant species in winter, but decreased in relative abundance to 2.3% and 0.7% respectively in summer (Appendix 1). Similarly, Cape White-eye *Zosterops virens* (16.5%) and Bar-throated Apalis *Apalis thoracica* (15.2%) were the most abundant species in summer but significantly less abundant in winter (Appendix 1). There was no significant change in 18 (45%) bird species, and statistical analysis of the remaining 11 species was limited by small sample sizes (Appendix 1).

A total of 50 bird species (25 families) were recorded in New Forest, of which 20 species were forest specialists (40% of the 50 species recorded and 42% of all known South African forest specialists; Table 2). There was an equal number of bird species in winter to summer (Table 2). This accounted for the greatest proportion of birds compared to generalist and visitor species in both seasons (Table 2). The majority of species (90%) were resident, supplemented by migrant species in summer (Table 2).

Table 2. Bird species richness in New Forest using incidence data (50 m radius).

Season	Richness	ICE	Forest specialist	Forest generalist	Forest visitor	R & M Richness	
						R	M
Combined	50	55 ± 0	20 (40)	11 (22)	19 (38)	45 (90)	5 (10)
Winter	37	42 ± 0.01	18 (49)	8 (21)	11 (30)	37 (100)	0
Summer	44	51 ± 0.01	18 (41)	11 (25)	15 (34)	39 (89)	5 (11)
Migrants Excluded	39	43 ± 0	17 (44)	10 (26)	12 (31)	39 (100)	0

[2]A comparison of bird species richness and estimated richness (mean ± SD) using the Incidence-Based Estimator (ICE) between bird recorded in combined seasons, winter and summer. The richness and proportion (%) of forest specialists, generalists, and visitors are indicated; as well as of resident (R) and migrant (M) species per season.

Bird species richness was significantly higher in summer than winter (Paired T-test; $t = 2.33$; $p < 0.05$; Table 2), despite the removal of migrant species from the summer analysis (Paired T-test; $t = 2.02$; $p < 0.05$). The Incidence-Based Estimator (ICE) of species richness demonstrated that not all species were recorded during the sampling sessions (Table 2). This was because the estimated species richness in both winter and summer was greater than the recorded species richness, of five and seven bird species for winter and summer respectively (Table 2). This is realistic because an extra seven and six species were recorded (outside of sampling sessions) in winter and summer respectively (Appendix 1).

Eleven species (22%) were recorded in only winter or summer, five of which were migrant species in summer (Appendix 1). Six resident species, such as Thick-billed Weaver *Amblyospiza albifrons* and Amethyst Sunbird *Chalcomitra amethystina* entered the forest seasonally (Appendix 1). Therefore, compositional changes were due to latitudinal and local movements of forest birds between seasons.

In terms of sampling completeness (Soberon *et al.* 2007), the estimated species richness using the Chao2 estimator (at a 95% C.I.) ranged from 38 to 53 species in winter

(40.0 ± 3.1) and 44 to 56 species (46.3 ± 2.4) in summer. Therefore, sampling completeness was estimated between 70 and 99% complete in winter (mean = 93%) and between 78 and 99% complete in summer (mean = 95%). Therefore, sampling effort was good but incomplete as not all species were recorded during the sampling sessions regardless of the additional 25 m band. Sampling completeness of forest generalists reached 100% in both seasons. However, the sampling completeness for winter specialists (mean = 93%; range 59 - 99%), summer specialists (mean = 97%; range 72 - 100%), winter visitors (mean = 97%; range 65 - 100%) and summer visitors (mean = 91%; range 55 - 99%) was low. Although sampling was > 90% complete for all bird categories, forest generalists were sampled most comprehensively compared to specialists and visitors.

2.4.2. Functional turnover

Feeding guilds were not equally represented in abundance between seasons where nectarivores (Wilcoxon Sign Test; $Z = 4.97$; $p < 0.01$), frugivores (Wilcoxon Sign Test; $Z = 2.53$; $p < 0.01$), and granivores (Wilcoxon Sign Test; $Z = 2.31$; $p = 0.02$) were significantly more abundant in winter; and omnivores (Wilcoxon Sign Test; $Z = 4.84$; $p < 0.01$) and insectivores (Wilcoxon Sign Test; $Z = 3.39$; $p < 0.01$) were significantly more abundant in summer (Figure 2).

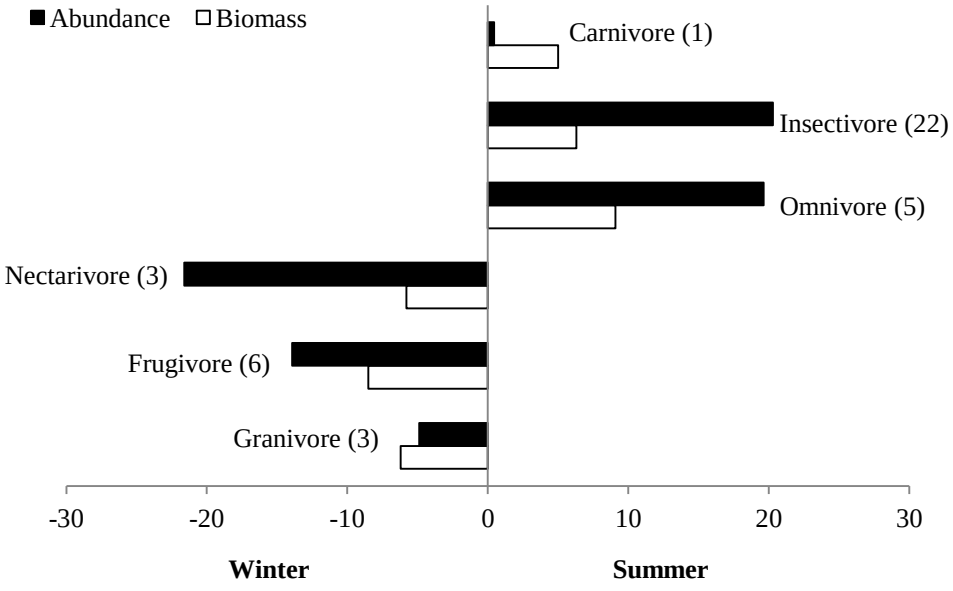

Figure 2. Proportional change (%) in the abundance and biomass of birds in different feeding guilds between seasons (n = 40 species). The number of species per guild is indicated.

There was a greater biomass (58.1%) of plant-eaters (frugivores, granivores, and nectarivores) in winter than summer, but a greater biomass of insect-eaters (insectivores and omnivores) in summer (57.4%) than winter (Figure 2). There was a slightly lower average biomass per area (986 ± 980 $g.ha^{-1}$) in winter than in summer (1067 ± 996 $g.ha^{-1}$; Wilcoxon Sign Test; Z = 0.13; n = 56; p = 0.90).

2.4.3. Flower and fruit production

There was a significant increase in overall flower density from winter to summer (Wilcoxon Sign Test; Z = 2.9; p < 0.01); however, there was no significant difference in fruit density between seasons (Table 3). When resource availability was assessed for food known to be consumed by birds, flower density decreased slightly from winter to summer but fruit density remained approximately the same (Table 3).

Table 3. Density (mean.m^{-2} ± SD) of flowers and fruit in winter and summer (n = 12).

	Resource	Winter	Summer	Z	P
Overall	Flower	1.6 ± 2.5	31.2 ± 26.7	2.9	< 0.01*
	Fruit	7.3 ± 17.8	5.0 ± 9.3	0.2	0.86
Birds	Flower	1.2 ± 2.3	0.1 ± 0.4	1.2	0.23
	Fruit	6.7 ± 16.4	5.0 ± 9.3	0.2	0.86

[3]'Overall' indicates total production of flowers and fruit. 'Birds' are only food eaten by birds (*p < 0.05).

Plants produced a higher abundance of fruit in winter (669 ± 3,197.4; N = 48 species) than summer (268.3 ± 1,191.1; N = 89 species). This was due to the mass contribution of fruit by canopy tree species, such as *Podocarpus latifolius* and *Celtis africana* (Table 4). However, fruit production was not significantly different between seasons (Wilcoxon Sign Test; Z = 0.9; p = 0.4).

Both canopy and understory plants produced fruit in both seasons (Table 4). However, canopy trees produced the highest proportion (89.2%) of fruit in winter as opposed to summer where understory plants produced the highest proportion (96.8%) of fruit (Table 4). The dominant flowering plant in winter was *Halleria lucida*, a canopy species, but understory plants produced the highest propotion of flowers in summer (Table 4).

Table 4. The relative abundance (RA; %) of flowers (FL) and fruit (FR) produced per plant species in winter (W) and summer (S) that are available to birds as a food source.

	Plant species	GF	n	Height (mean ± SD)	RA (%)	Crop/plant (mean ± SD)	Crop range (min - max)
WFL	*Halleria lucida*	ET	4	14.3 ± 2.9	100	1,452.5 ± 891.6	200 - 1,610
WFR	*Podocarpus latifolius*	ET	7	12.8 ± 5.7	81.6	3,744.3 ± 8,130.3	40 - 22,100
	Pyracantha angustifolia [I]	ES	1	5.0	6.9	2,200	2,200
	Celtis africana	DT	2	15.5	6.6	1055	1,010 - 1,100
	Carissa bispinosa	ES	24	3.2 ± 1.1	1.7	23.3 ± 27.3	10 - 120
	Eugenia zuluensis	ET	2	4.8 ± 1.8	0.7	110	10 - 210
	Calodendrum capense	DT	2	15.0	0.7	105	100 - 110
	Behnia reticulata	EC	1	4.0	0.6	200	200
	Unidentified Vine	DC	1	5.0	0.4	120	120
	Coccinia palmata	DC	1	5.0	0.3	110	110
	Kiggelaria africana	DT	1	10.0	0.3	100	100
	Asparagus sp.	EC	3	1.0	0.1	13.3 ± 5.8	10 - 20
	Gymnosporia harveyana	ES	2	3.1	0.1	10	10
	Solanum acanthoideum	ES	1	1.5	0.03	10	10
SFL	*Sclerochiton odoratissimus*	ES	5	1.9 ± 0.3	82	100	100
	Scutia myrtina	EC	2	0.6	18	55	10 - 100
SFR	*Searsia pyroides*	ET	1	6.0	46	11,000	11,000
	Asparagus sp.	EC	30	1.3 ± 0.7	18.8	131.3 ± 396.3	10 - 2,000
	Carissa bispinosa	ES	39	2.7 ± 0.8	13.7	83.9 ± 79.8	10 - 310
	Gymnosporia harveyana	ES	8	3.2 ± 1	6.9	205 ± 367.7	10 - 1,100
	Scutia myrtina	EC	2	3.5	5.5	655	200 - 1,110
	Unidentified Tree	T	2	5.5	5	600	200 - 1,000
	Celtis africana	DT	1	14.0	4	1,000	1,000
	Calodendrum capense	DT	1	16.0	0.8	200	200
	Rubus spp. [I]	DS	2	1.6	0.5	55	10 - 100
	Kiggelaria africana	DT	1	10.0	0.4	100	100
	Solanum acanthoideum	ES	1	1.8	0.4	100	100
	Halleria lucida	ET	1	14.0	0.04	10	10[4]

[4]The growth form (GF) is indicated for evergreen (E) and deciduous (D) trees (T), shrubs (S), and climbers (C) (Pooley 2005; Boon 2010). Plant species ≥ 8 m tall are canopy species. An 'I' indicates invasive plants. Species ordered according to RA.

2.4.4. Invertebrate diversity

Invertebrate diversity and estimated species richness were estimated to be significantly higher in summer than winter (Table 5).

Table 5. A comparison of the estimated invertebrate richness and Shannon-Weiner diversity between winter and summer (EstimateS; Colwell 2006).

	Winter	Summer	t	df	P
Abundance-Based Estimator	168.5	219.2	3.2	79	0.00*
Chao1 estimator	169.9 ± 24.4	199.0 ± 20.0	2.7	79	0.01*
Shannon-Wiener diversity	3.2	4.0	6.1	79	0.00*

2.5. Discussion

2.5.1. Bird community dynamics

While Afromontane forests are generally species poor (Eeley *et al.* 2001), the bird species richness in New Forest was relatively high compared to other Afromontane forests in South Africa (Cody 1983; Koen 1992; Wethered and Lawes 2003; Wethered and Lawes 2005). However, species richness was not constant. Several species were common between seasons but there was a greater diversity, richness, and abundance of forest birds in summer than winter. The breeding months of forest birds are between November and March (Wethered and Lawes 2003). Breeding migrants, such as African Emerald Cuckoo *Chrysococcyx cupreus*, contributed to the higher bird diversity in summer. However, migrant birds only comprised 10% of the total species richness and < 1% of the abundance, of forest birds in summer. Therefore, local or altitudinal movements of resident birds are the most important drivers of compositional change in a forest bird community between seasons. Many residents, such as Southern Double-collared Sunbird *Cinnyris chalybeus*, Thick-billed Weaver *Amblyospiza albifrons*, and Amethyst Sunbird *Chalcomitra amethystina*, conduct local seasonal movements and track available food resources (Fleming 1992; Craig and Hulley 1994; Hockey *et al*. 2005). Breeding requirements and environmental factors also have an influence on the local movement patterns of birds (Fleming 1992). Thick-billed Weaver, for example, foraged in the forest in winter but moved to reed beds in summer to breed (Hockey *et al.* 2005), whereas, water-associated species, such as Mountain Wagtail *Motacilla clara* and African Fish-Eagle *Haliaeetus vocifer*, were most likely recorded in summer because of the increased water flow in the Umgeni River which provided additional foraging opportunities for these species (Skead 1964; Symes *et al.* 2002). This pattern demonstrated the dynamic nature of the forest bird community and has important implications for community composition (Hockey *et al.* 2005).

Forest specialists comprised the largest proportion of both communities, and together with generalists, made up three quarters or more of each community. There was a relatively high proportion, (but not necessarily a higher richness), of forest specialists compared to other forests in South Africa (e.g. Symes *et al.* 2000; Symes *et al.* 2002; Wethered and Lawes 2003; Brown 2006). Although forest specialists have been described as reluctant to cross gaps between forest patches (Oatley 1989) there was a discernible turnover in forest specialists because 63% of species that were significantly more abundant in summer were forest specialists. Possibly these forest specialists are not as stationary as previously thought, but move between forest patches in search of food or other requirements when necessary. There was a greater abundance of visitors in the forest in summer. The influx of visitors consequently diluted the proportion of forest specialists in the wet season, a finding similar to Brown (2006).

The sampling completeness of specialists was lower than the generalists, particularly in winter. This may have been because forest specialists call less in the non-breeding season, and therefore become more cryptic. The sampling completeness of visitors was particularly low, probably because forest is not their preferred habitat and so sampling completeness will never be comprehensive. A high proportion of forest specialists and generalists in the forest demonstrated that, although this forest patch was disturbed in the past, as indicated by the high density and low diameter at breast height (DBH) of trees (Downs and Symes 2004), currently there is lower anthropogenic disturbance in the forest patch (Carlson 1986; Wethered and Lawes 2003). Maintaining the integrity of indigenous forest therefore is important for the survival of forest taxa (Castley and Kerley 1996), particularly forest specialist and generalist species.

2.5.2. Food availability and bird dynamics

Numerous plants in tropical forests flower or fruit in the dry season providing important resources to nectarivores and frugivores, whereas wind- and insect-pollinated flowers are produced in the wet season (Koen 1992; Murali and Sukumar 1994; Mac Nally and McGoldrick 1994; Borghesio and Laiolo 2004). This trend was evident in New Forest, however, one of the key differences in the seasonal flowering and fruiting phenology was the stratum in which food was produced. *Halleria lucida* is often an understory plant, but was a canopy species in this study. It was the most important flowering plant to nectar-feeders, such as Southern Double-collared Sunbird *Cinnyris chalybeus* and Greater Double-collared

Sunbird *Cinnyris afer*, in winter (Skead 1964). In summer, however, understory plants like *Sclerochiton odoratissimus* (shrub) and *Scutia myrtina* (scrambling shrub or climber), were the dominant flowering plants and nectar source for birds. These plants, however, are not the preferred food source of nectarivores, and their size and white floral colour suggests insects as their main visitor (SLS *pers. obs.*). This finding was similar to studies elsewhere, as many tropical forests produce the highest abundance of nectar-producing flowers in the dry season with an associated increase in nectarivores abundance (Pearson 1977; Frost and Frost 1980; Fleming 1992; Murali and Sukumar 1994; Borghesio and Laiolo 2004).

Canopy trees, such as *Podocarpus latifolius* and *Celtis africana*, produced the highest relative abundance of fruit in the dry season, attracting gregarious frugivores, such as Dark-capped Bulbul *Pycnonotus tricolor* and Sombre Greenbul *Andropadus importunus*. Understory plants produced the highest relative abundance of fruit in summer which may have been a more important food source for omnivores, such as Cape White-eye *Zosterops virens* and Southern Boubou *Laniarius ferrugineus*. Although, specific crop abundance changed between seasons and strata, flower and fruit were present in both seasons and in all strata, as in the forests of northern Kenya (Borghesio and Laiolo 2004). This is important for forest resident frugivore specialists, such as Knysna Turaco *Tauraco corythaix* and Bush Blackcap *Lioptilus nigricapillus*. Lastly, the fruit produced by several plant species in summer, such as *C. africana* were still unripe at the time of data collection (SLS *pers. obs.*), whereas in winter the old fruit was consumed by granivores and frugivores, such as Thick-billed Weaver and Knysna Turaco (SLS *pers. obs.*). Fruit- and nectar-feeding species are generally represented by a low species richness, but are abundant and characterised by strong seasonal variations in abundance (Poulin *et al.* 1994). Therefore, the forest acts as a refuge to guilds that rely on spatially limited or ephemeral resources, as produced by *H. lucida* and *P. latifolius* in winter. In addition, the wider movements of these more mobile species may also be important in maintaining active links between forests through seed dispersal.

There was an overall significant increase in flower density in the wet season due to mass flowering of the forest floor annuals. These flowers are insect-pollinated, and therefore, in combination with greening of the forest deciduous species, provide a substantial resource to invertebrates in the wet season (Pearson 1977; Murali and Sukumar 1994; Borghesio and Laiolo 2004). There was a likewise increase in the diversity and biomass of birds, particularly insect-eaters, in summer than winter. This change was mainly evident in smaller insectivorous species, such as Bar-throated Apalis *Apalis thoracica* and Yellow-throated Woodland Warbler *Phylloscopus ruficapilla*. All migrant birds were insectivorous and

therefore contributed to the proportional increase in insectivores in summer. In addition, all forest specialist and visitor species that increased significantly in summer were insect-eaters. Insect-eating guilds responded to invertebrate availability whilst nectarivores in this study responded to changes in their nectar food sources rather than invertebrates, which they do include in their diet (also see Koen 1988b; Koen 1992). Omnivores probably increased in summer due to an increase in both invertebrate and fruit abundance in the understory. Many of these species are also able to diet-switch in response to a seasonal change in resource dominance (Koen 1992; Borghesio and Laiolo 2004). Therefore, an increase in invertebrates and understory fruit in summer provided additional resources to omnivores.

2.6. Conclusion

Food availability is a keystone element in seasonal community changes especially in terms of functional turnover. Further, a shift in resource availability between strata favours the presence of particular feeding guilds at certain times of the year. Due to the mass contribution of flowers and fruit during the dry season, the forest may act as a refuge for frugivores and nectarivores that track patchily distributed food resources. Conversely, an increase in forest productivity in summer serves to increase the capacity of the forest to support more species, particularly insect-eaters, many of which were specialist and generalist species. This seasonal shift in food availability contributes to the turnover in composition and function of the forest bird community, particularly of resident species. The wider movements of these more mobile species between patches allow them to track the ephemeral patterns of food availability. In addition, they may also be important in maintaining active links between forests through seed dispersal. Therefore, conservation of a local network of forest patches is important to maintain movement patterns and the community dynamics of forest birds, particularly specialists and generalists that respond in different ways to the seasonal changes in food resources.

2.7. Acknowledgements

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2.9. Appendix 1

A species list of forest birds recorded in winter (W, July/August 2010) and summer (S, January/February 2011) in New Forest, KwaZulu-Natal. The total and relative abundance (RA, %) of birds is given (25 m radius only) and the three highest RA values per season are underlined (*p < 0.05). Defined feeding guilds (FG) and the movements and migrations (M&M) of birds are provided.

Bird species	FG	W	S	Z	p	M&M
Long-crested Eagle *Lophaetus occipitals* [f]	C	-	O			R
Martial Eagle *Polemaetus bellicosus* [f]	C	P	O			R
African Fish-Eagle *Haliaeetus vocifer* [f]	C	-	O			R
African Goshawk *Accipiter tachiro*	C	O	2 (0.5)	-	-	R
Amur Falcon *Falco amurensis* [f]	I	-	O			M
African Olive-Pigeon *Columba arquatrix* [F]	F	1 (0.3)	O	-	-	R,LM
Red-eyed Dove *Streptopelia semitorquata* [f]	G	O	O			R
Cape Turtle-dove *Streptopelia capicola* [f]	G	O	P			R
Tambourine Dove *Turtur tympanistria*	G	P	-			R
Lemon Dove *Aplopelia larvata*	G	2 (0.6)	O	-	-	R
Knysna Turaco *Tauraco corythaix*	F	6 (1.7)	6 (1.4)	0.1	0.95	R
Red-chested Cuckoo *Cuculus solitarius* [F]	I	-	O			M
Black Cuckoo *Cuculus clamosus* [f]	I	-	P			M
African Emerald Cuckoo *Chrysococcyx cupreus*	I	-	1 (0.2)	-	-	M
Narina Trogon *Apaloderma narina*	I	O	P			R
Red-fronted Tinkerbird *Pogoniulus pusillus* [F]	F	P	3 (0.7)	1.6	0.11	R
Olive Woodpecker *Dendropicos griseocephalus*	I	4 (1.1)	9 (2.0)	1.2	0.24	R
Red-throated Wryneck *Jynx ruficollis* [f]	I	1 (0.3)	-	-	-	R
Black Saw-wing *Psalidoprocne holomelas* [f]	I	-	O			M
Black Cuckooshrike *Campephaga flava* [F]	I	P	P			R,M
Grey Cuckooshrike *Coracina caesia*	I	O	12 (2.7)	2.8	0.01*	R
Fork-tailed Drongo *Dicrurus adsimilis* [f]	I	1 (0.3)	7 (1.6)	1.8	0.08	R
Black-headed Oriole *Oriolus larvatus* [f]	I	O	4 (0.9)	1.6	0.11	R
Southern Black Tit *Parus niger* [f]	I	-	1 (0.2)	-	-	R
Bush Blackcap *Lioptilus nigricapillus*	F	P	1 (0.2)	-	-	R,AM
Dark-capped Bulbul *Pycnonotus tricolor* [f]	F	<u>38 (10.8)</u>	3 (0.7)	3.6	0.00*	R
Terrestrial Brownbul *Phyllastrephus terrestris* [F]	I	10 (2.8)	20 (4.5)	1.0	0.31	R
Sombre Greenbul *Andropadus importunus* [F]	F	<u>40 (11.4)</u>	32 (7.2)	1.1	0.27	R
Olive Thrush *Turdus olivaceus* [F]	I	36 (10.2)	1 (0.2)	3.4	0.00*	R,AM
Chorister Robin-Chat *Cossypha dichroa*	O	2 (0.6)	10 (2.3)	1.8	0.07	R,AM
Cape Robin-Chat *Cossypha caffra* [f]	O	9 (2.6)	2 (0.5)	1.8	0.07	R,AM

Bird species	FG	W	S	Z	p	M&M
White-starred Robin *Pogonocichla stellata*	I	7 (2.0)	4 (0.9)	0.8	0.44	R,AM
Yellow-throated Woodland-Warbler *Phylloscopus ruficapilla*	I	20 (5.7)	45 (10.2)	2.9	0.00*	R,AM
Bar-throated Apalis *Apalis thoracica*	I	24 (6.8)	67 (15.2)	3.9	0.00*	R
Yellow-breasted Apalis *Apalis flavida* [f]	I	2 (0.6)	21 (4.8)	2.8	0.01*	R
Green-backed Camaroptera *Camaroptera brachyura*	I	1 (0.3)	22 (5.0)	3.5	0.00*	R
Neddicky *Cisticola fulvicapilla* [f]	I	P	-			R
African Dusky Flycatcher *Muscicapa adusta* [F]	I	-	2 (0.5)	-	-	R,AM
Cape Batis *Batis capensis*	I	22 (6.3)	29 (6.6)	0.6	0.58	R
Blue-mantled Crested Flycatcher *Trochocercus cyanomelas*	I	8 (2.3)	2 (0.5)	1.6	0.11	R,AM
African Paradise-Flycatcher *Terpsiphone viridis* [f]	I	-	6 (1.4)	2.0	0.04*	M
Mountain Wagtail *Motacilla clara* [F]	I	1 (0.3)	4 (0.9)	1.1	0.29	R
Southern Boubou *Laniarius ferrugineus* [F]	O	O	6 (1.4)	1.8	0.07	R
Black-backed Puffback *Dryoscopus cubla* [F]	I	2 (0.6)	8 (1.8)	1.8	0.08	R
Olive Bush-Shrike *Telophorus olivaceus*	I	1 (0.3)	P	-	-	R
Red-winged Starling *Onychognathus morio* [f]	O	O	-			R,AM
Southern Double-collared Sunbird *Cinnyris chalybeus*	N	80 (22.7)	10 (2.3)	4.8	0.00*	R,LM
Greater Double-collared Sunbird *Cinnyris afer* [F]	N	8 (2.3)	2 (0.5)	1.3	0.21	R
Amethyst Sunbird *Chalcomitra amethystina* [f]	N	-	3 (0.7)	-	-	R,LM
Collared Sunbird *Hedydipna collaris*	O	6 (1.7)	21 (4.8)	2.0	0.04*	R
Cape White-eye *Zosterops virens* [f]	O	3 (0.9)	73 (16.5)	4.8	0.00*	R
Thick-billed Weaver *Amblyospiza albifrons* [f]	G	4 (1.1)	-	-	-	R,LM
Dark-backed Weaver *Ploceus bicolor*	I	1 (0.3)	2 (0.5)	0.5	0.59	R
Common Waxbill *Estrilda astrild* [f]	G	-	P			R
Swee Waxbill *Coccopygia melanotis* [f]	G	P	-			R,AM
Forest Canary *Crithagra scotops*	G	12 (3.4)	1 (0.2)	1.6	0.11	R

[5]The 'O' indicates bird species recorded within the 25 - 50 m radius only; 'P' represents species that were present in the forest, but not recorded during sampling sessions, and '-' represents species that were not detected in the forest at any stage. Forest specialists are bold and forest generalists (F) and forest visitors (f) are indicated. Defined feeding guilds (FG) were carnivore (C), insectivore (I), omnivore (O), nectarivore (N), frugivore (F) and granivore (G). The movements and migrations (M&M) included resident (R), local seasonal movements (LM), latitudinal migration (M), and altitudinal migration (AM) (Johnson and Maclean 1994; Hockey *et al.* 2005).

Chapter 3: Food limitation and foraging behaviour

http://www.talking-naturally.co.uk/white-starred-robin-nairobi/

Seasonal changes in food limitation drive the foraging behaviour and functional dynamics of an Afromontane forest bird community

Samantha L. Scott* and Craig T. Symes

School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, P/Bag 3, Wits 2050, South Africa

* Corresponding author

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***Corresponding author:**

Samantha L. Scott

School of Animal, Plant and Environmental Sciences

University of the Witwatersrand

Private Bag 3

Wits, 2050

South Africa

Email: samantha.scott@students.wits.ac.za

Telephone: +27 (0)11 717-6478

Facsimile: +27 (0)11 717-6494

3.1. Abstract

The foraging ecology of birds was assessed in response to seasonal changes in vegetation structure and food abundance in a forest patch. Bird foraging behaviour and the vertical height profile of vegetation cover, flower and fruit availability were recorded in 400 m^2 quadrats. Data were collected in winter and re-sampled in summer. Nectarivores, omnivores, and insectivores tracked the seasonal height distribution of food between the canopy and lower strata, but frugivores did not. In winter, birds exploited approximately twice the number of resource pools than in summer. In addition, resource partitioning between bird species was high and niche similarity was low. In summer, however, there was high niche overlap in pool exploitation between bird species, particularly within insectivores and nectarivores. This was because food resources were limiting in the dry season but more abundant in summer. Therefore, birds compensated for reduced food availability through niche expansion in one or more dimensions in winter but in summer niche width contracted as individuals selected preferred food resources. Frugivores were the exception because fruit was highly abundant in winter and therefore niche width expanded to obtain fruit from various plant species. In conclusion, birds became generalist feeders in a food-limited season. This was possibly to, 1) fulfil nutritional requirements, and 2) limit direct competition between intra-guild species that are competing for the same resource. However, seasonal food limitation is species-dependent.

Keywords: Afromontane forest birds, food distribution, seasonal food limitation, resource partitioning, niche separation

3.2. Introduction

Most animals occupy a shared environment, in which several species interact directly or indirectly (Perrins and Birkhead 1983; Walther 2002). In terrestrial environments, food is often considered an important limiting resource to birds (Holmes and Recher 1986). Forests have a complex, multilayered structure where plant composition determines both the structural heterogeneity and food availability that support a diversity of bird species (MacArthur and MacArthur 1961; Hopkins 1977; Robinson and Holmes 1984; Holmes 1986; Holmes and Recher 1986; Mucina and Geldenhuys 2006). The vertical layers in a forest provide foraging opportunities for birds that are morphologically adapted for exploiting prey

on particular substrates (Holmes *et al.* 1979; Miles and Ricklefs 1984; Symes *et al.* 2002). However, there is often seasonal variation in both vegetation structure and food production (Fogden 1972; Murali and Sukumar 1994; Borghesio and Laiolo 2004). A seasonal change in fruit, flower, and invertebrate availability as well as the morphological and behavioural characteristics of the birds themselves, influence the degree to which birds exploit food resources (Frost and Frost 1980; Robinson and Holmes 1982; Perrins and Birkhead 1983; Herrera *et al.* 2005). Some birds compete for the same food resources, and the pattern of resource exploitation and the competitive methods that maintain these patterns, depends largely on the quantity and quality of a resource over space and time (Frost and Frost 1980; Perrins and Birkhead 1983; Fleming 1992; Wirminghaus *et al.* 2001; Newton 2003).

A species that cannot adapt to competition for a resource, and hence co-exist with a competitor, will be displaced or extirpated from an area (Gause 1934; Perrins and Birkhead 1983). The ultimate division of food resources between co-existing species is termed resource partitioning, and inter-specific competition is considered to be one of the dominant processes in which ecologically similar species partition resources (Schoener 1974). A niche is the space that a species occupies within a biotic environment that is different, in some way, from its co-occurring competitors within the community (Elton 1927; Hutchinson 1957; Wiens 1989). Species cannot co-occur if they occupy the same niche and therefore ecologically similar species co-exist through niche differentiation in which niche size, shape, location, and overlap (niche similarity) vary in response to changes in competitive pressure (Gause 1934; Hutchinson 1957; Wiens 1989). Therefore, in order for ecologically similar bird species to co-exist, there has to be some level of partitioning where species differ in patch use in several ways including food selection or adopting foraging strategies that are advantageous over a competitor (Gause 1934; Perrins and Birkhead 1983; Walther 2002). This is the Gause Principle or Competitive Exclusion Principle (Gause 1934; Hardin 1960). Niche similarity, for example, may increase during periods of increased food abundance as species can select preferred food resources (Wiens 1989); however, it should be noted that there are several dimensions to a niche where there may be high overlap in one dimension but not in another (Wiens 1989).

A seasonal change in food availability has implications for the foraging behaviour and foraging success of birds within a forest patch. Understanding the foraging ecology of birds in response to changes in vegetation structure and food availability is important because it has implications for forest management and conservation, particularly to conserve bird diversity as well as seasonal patterns and processes. However, few studies in southern African and

African forests have assessed food partitioning and niche differentiation in forest birds (but see Cody 1983; Koen 1988; Koen and Crowe 1987; Earlé 1989; Koen 1992). If it is assumed that all species that have competed unsuccessfully for a food resource in the past have been extirpated from the forest patch, it can likewise be expected that all species sharing a forest patch co-exist with minimal or reduced conflict for resources. This is done through various mechanisms, such as vertical stratification, adoption of specific forage manoeuvres, plant selection, or forage heights that are different from a competitor (e.g. Maurer and Whitmore 1981; Holmes 1986; Holmes and Recher 1986; Holmes and Schultz 1988; Koen 1988). The aim of this study was to assess the foraging ecology of birds, in response to seasonal variation in food abundance and vegetation cover, in an Afromontane forest patch. Specifically, this study assessed, 1) the vertical stratification of foraging birds, in response to seasonal changes in vegetation structure and available food resources; 2) the seasonal division of food resources within each feeding guild; and 3) niche similarity in terms of manoeuvre, forage substrate, and forage height between bird species.

3.3. Methods

3.3.1. Site description

Data were collected during winter (15 July to 22 August 2010) and summer (16 January to 26 February 2011) in a 112.3 ha forest patch (Cooper 1985) on the privately owned New Forest Farm (29°27'53"S 29°52'54"E; *c.* 1,380 - 1,740 m a.s.l.), KwaZulu-Natal, South Africa (Figure 1). New Forest is an Afromontane Mist Belt Mixed *Podocarpus* Forest patch that consists of tall evergreen and deciduous trees (*c.* 15 - 20 m) and is multilayered with a dense understory and a well-developed herbaceous layer on the forest floor (Mucina and Geldenhuys 2006). There are several natural openings in the forest in which a dense layer of wetland plant species such as *Cyperus* and *Kniphofia* spp. grow. These areas are enclosed by stands of *Leucosidea sericea*. Precipitation in the Southern Mist Belt Forest region is *c.* 1,000 mm per annum with a distinct dry and wet season. Mist Belt forests in the austral winter receive < 50 mm rainfall per month but receive > 100 mm in summer where frequent mist supplements rainfall considerably (Mucina and Geldenhuys 2006). For additional details on the study site, see Chapter 2.

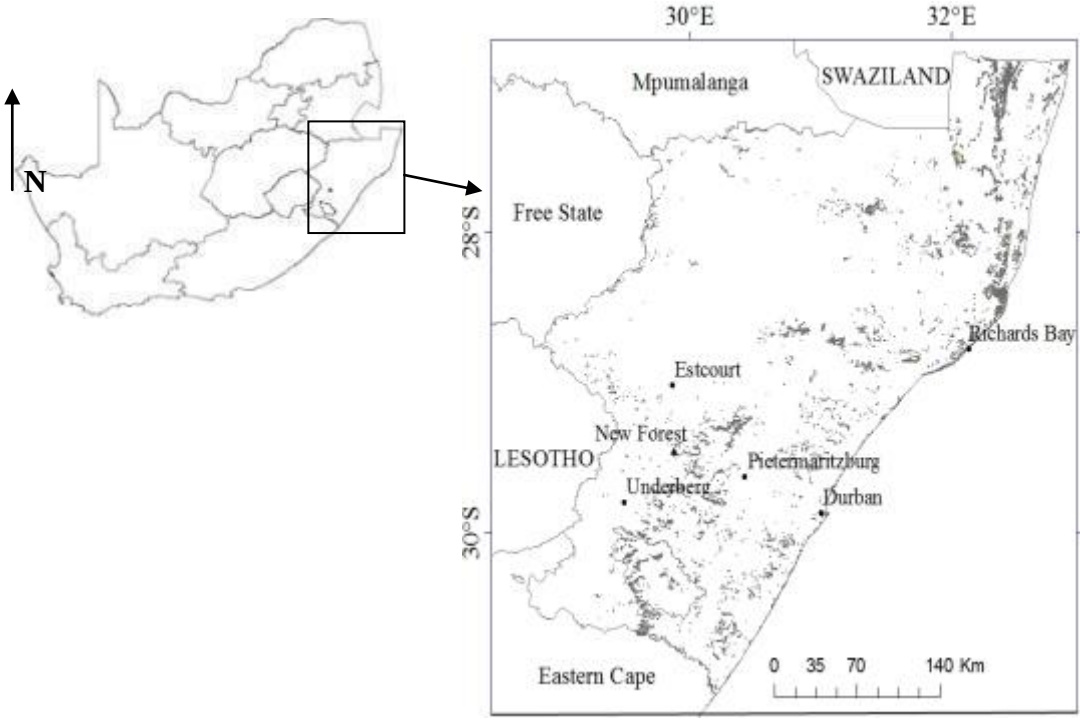

Figure 1. The position of New Forest (triangle) within indigenous forest (grey shading) in KwaZulu-Natal, South Africa [*Source*: Department of Agriculture, Fisheries and Forestry (DAFF) in South Africa]. Selected towns (dots), neighbouring provinces, and countries (uppercase) are for reference purposes. Inset: The location of KwaZulu-Natal in South Africa.

3.3.2. Field observations

Twelve 20 x 20 m (400 m^2) quadrats were distributed ≥ 60 m from one another throughout the forest in which to observe bird behaviour and to record vegetation structure and food availability in winter and summer (modified from Krüger and Lawes 1997). Quadrats were selected based on the homogeneity of slope, aspect, and vegetation within each quadrat and marked with a Global Positioning System (GPS) receiver at the centre and flagging tape at the corners. Quadrats were designated so that the same sites could be re-sampled in summer. Vertical strata were broadly defined as ground 0 m, understory 0 - 8 m, and canopy > 8 m (modified from Borghesio and Laiolo 2004).

3.3.2.1. Vegetation cover

To assess the vertical structure of the forest, vegetation cover (%) was measured along a Vertical Height Profile (VHP) at designated height intervals (m): 0 - 1, 1 - 2, 2 - 5, 5 - 10, 10

- 15, and 15 - 20 m (modified from Schemske and Brokaw 1981). Two 2 m poles were held erect and 4 m apart. Five VHP were measured randomly per quadrat (n = 60 per season). Ground cover (%) of grass, forbs, soil, leaf litter, dead wood, and rocks, was recorded within five randomly placed 1 m^2 quadrats per 400 m^2 quadrat (n = 60 per season). Grass and forb height (m) was recorded to assess available structure for forest floor bird species.

3.3.2.2. Flower and fruit availability

All flower- and fruit-producing plants were identified to species level. Food available in the form of nectar (estimated as flower abundance, and hereafter termed 'flowers'), and whole fruit were estimated per height interval in terms of defined categories: 0 - 10, 10 - 100, 100 - 1,000, and 1,000 - 10,000. This is because it was difficult to count abundance accurately in the forest, particularly in the upper height classes. Only tree species that provided a food resource to birds and with at least half of the trunk within the quadrat were considered.

3.3.2.3. Invertebrate sampling

Invertebrate sampling occurred over three days within six quadrats. To sample ground invertebrates, five pitfall traps, (white plastic cups 108 x 60 mm), were buried flush with the ground surface and ≥ 5 m apart in a quadrat (n = 30 per season). Each trap was filled with a non-toxic surfactant solution (1 drop dishwashing liquid per 1 L tap water) to ensure entrapment. To sample understory invertebrates, commercially available 90 x 150 mm AgriBiol® "bug traps" (Vlaeberg, South Africa) coated with a non-toxic glue (one blue and one yellow) were fastened to a tree trunk or branch with rope, at 1 m and 3 m facing north. Four traps were set up per quadrat (n = 24 per season). All traps were checked on consecutive mornings. All invertebrates were removed and stored in 75% alcohol. Sweep netting was done for five minutes each day (*c.* 30 - 50 sweeps per minute depending on openness of vegetation) within ≤ 2 m of the forest. This was enough time to sample the entire quadrat. All traps were removed after three days and replaced in summer, as required by the landowner.

3.3.2.4. Bird observations

The start and end time for each sampling session in a quadrat as well as the actual time (s) that an individual was observed for, was recorded. Bird foraging behaviour included active searching for, or ingesting, food. The minimum and maximum forage height (m) of birds, and the forage substrate, was recorded. Forage substrate was categorized as air; ground (including

leaf litter, rocks or dead wood); leaves; and bark or lichen on a twig (< 1 cm in diameter), branch (> 1 cm in diameter), trunk, or vine (modified from Snow and Snow 1971; Borghesio and Laiolo 2004). The manoeuvre that an individual used to obtain a resource and, if possible, the food item, was recorded (Table 1).

Table 1. List of manoeuvres employed by forest birds to search for and obtain food from a substrate or surface (Robinson and Holmes 1984; Holmes and Recher 1986; Holmes and Robinson 1988). Note: fruit- and nectar-feeders also consume insects when available.

Manoeuvre	Definition
Pounce	Bird captures animal prey with its feet as it lands on a substrate, typically the ground.
Sift	A flicking motion used to search through leaf litter in search of insects or fruit.
Glean	Perched bird picks stationary invertebrate prey from a nearby substrate. No flight is involved for either bird or invertebrate.
Hawk	Bird flies out from a perch, up or down, to capture air-borne invertebrate prey.
Probe	Bird inserts beak into opening in wood to capture an invertebrate, or flowers for nectar.
Hover	Bird flies out to snatch invertebrates or fruit from a substrate, excluding air. It may pause and hover shortly at a substrate or snatch the prey from a substrate as it passes.
Hang	Bird hangs upside down, tears apart or manipulates substrate for invertebrates or fruit.
Pluck	Bird thrusts its head forward to acquire a fruit and swallows it whole (Foster 1987).
Bite	Bird acquires a portion of a large fruit by biting it and swallowing pieces at a time rather than the whole fruit (modified from Foster 1987).
Peck	Bird walks quickly over the ground and picks seeds from the surface as it moves (modified from Koen 1988).

Sampling effort was calculated as the number of half-days in the field per season (Symes *et al.* 2002). A half-day is any period greater than one hour from dawn to dusk, and noon separates the day into morning and afternoon half-days (Symes *et al.* 2002). Both sampling effort and the total number of sampling hours in the quadrats were greater in summer than winter (Table 2). The daily sampling sessions started and ended earlier in summer, however, the timeframe was similar between winter (10h14min) and summer (10h57min). This was because the sun rose *c.* 1.5 hours earlier in summer than winter (Table 2). However, the majority of observations were made before noon in both seasons (Table 2). Heavy mist in the morning and afternoon, sometimes over an entire day, in either season, and additional heavy rain in the afternoons in summer, affected the number of hours spent in the

forest. Therefore, behaviour was also recorded while walking between quadrats to increase the number of behavioural observations, and the location was marked with a GPS.

Table 2. Observation hours spent in New Forest between winter and summer. Sampling effort is the number of half-days per season (Symes *et al.* 2002). Sampling was between dawn and dusk [*source daylight hours:* South African Weather Services for KwaZulu-Natal]. Average time per quadrat was similar between seasons and sampling was most frequently conducted before noon. The frequency (and proportional frequency %) of observations per timeframe are provided. The total number of foraging observations and the number of species observed is given per season.

	Winter	**Summer**
c. daylight hours (sunrise to sunset)	6:50 - 17:30	5:30 - 19:00
Daily sampling range (min - max)	7:08 - 17:22	5:43 - 16:00
Observations (quad only)		
Half-days	27	31
Total hours	64.4	88.3
Mean ± SD (min/quad)	50.2 ± 16.9 (n = 77)	54.6 ± 9.5 (n = 97)
sunrise - 9:00	39 (25)	54 (28)
9:00 - 12:00	61 (40)	70 (36)
12:00 - 15:00	43 (28)	62 (31)
15:00 - end	11 (7)	10 (5)
Total foraging observations	248 (29)	266 (28)
Observations (forest total)		
Total hours	66.1	88.5
Total foraging observations	339 (30)	305 (31)

3.3.2.5. Data analysis

All data were tested for normality prior to any statistical analyses, which were conducted in Statistica 6.1.478.0 (Statsoft. Inc. 2004) unless otherwise stated. Only the data collected from quadrats were utilised. One-way ANOVA tested for significant changes in vegetation cover between seasons and a Wilcoxon Sign Test tested for seasonal changes per stratum. Seasonal changes in bird stratification were tested using a Chi-square test. The relationship between vegetation cover and the relative abundance of foraging birds was assessed using a

Spearman's Rank Correlation. A Paired T-test tested for seasonal differences in both forb cover and height. A Sign Test tested for significant differences in flower and fruit abundance produced < 5 m and > 5 m. A Mann-Whitney U Test tested for significant shifts in the height of manoeuvre employment between winter and summer. A Kruskal-Wallis Test tested for significant differences in invertebrate abundance between trap methods and a Wilcoxon Sign Test tested for significant differences in invertebrate abundance per trap between seasons.

A hierarchical cluster analysis was used to demonstrate resource partitioning between bird species based on the use (1) or not (0) of a manoeuvre (Primer 6.1.5; Clarke and Gorley 2006). Feeding guilds were defined based on dietary information (Hockey *et al.* 2005; also see Chapter 2). Manoeuvre and forage substrate were combined to define a set of 'resource pools' exploited by bird species in a season. A non-metric Multi-Dimensional Scaling (MDS) plot was used to assess niche similarity based on the average forage height at which various pools were exploited (Primer 6.1.5; Clarke and Gorley 2006). The feeding guild, number of observations, average forage height (m), and manoeuvre employed by a species is summarised in Appendix 1.

3.4. Results

3.4.1. Vegetation structure and foraging birds

Vegetation cover increased significantly from winter to summer (One-way ANOVA $F_{(5, 354)} = 25.0$; $p < 0.01$; Figure 2). The greatest increase in vegetation cover was between 0 - 1 m and 5 - 10 m by *c.* 10 - 15% (0 - 1 m: $Z = 4.5$, $p < 0.01$; 5 - 10 m: $Z = 3.3$, $p < 0.01$; Figure 2). There was a significant increase in the foraging distribution of birds from the dry to wet season, ($\chi^2 = 136.5$, df = 5; $p < 0.01$; n = 60), particularly between 2 - 5 m (Figure 2). In contrast, vegetation cover increased significantly between 0 - 1 m from winter to summer, but bird foraging frequency significantly decreased (Figure 2). Bird foraging distribution was significantly correlated with vegetation cover in both winter (Spearman = 0.6, $p < 0.05$) and summer (Spearman = 0.8, $p < 0.05$; Figure 2).

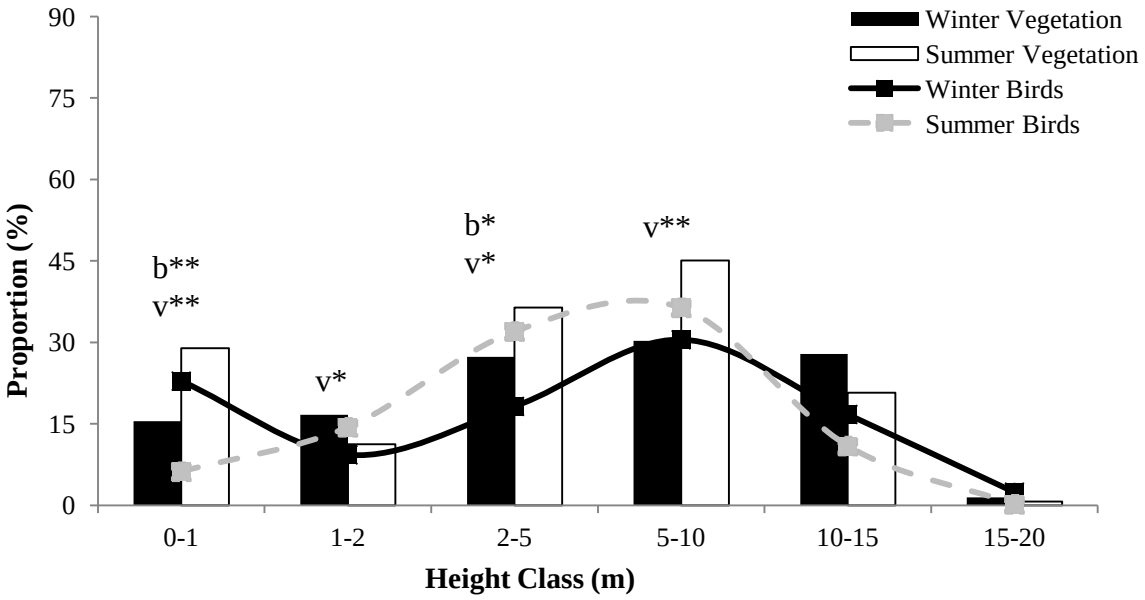

Figure 2. Vegetation Height Profile (VHP) of vegetation cover (%) between winter and summer (n = 60 per season). The relative frequency (%) of foraging birds per stratum (winter n = 339; summer n = 305 observations) was plotted against vegetation cover. Asterisk shows a significant seasonal change in vegetation (v) cover and bird (b) frequency (*p < 0.05; ** p < 0.01).

There was a low proportion (38%) of herbaceous ground cover and a high proportion of non-vegetated ground (62%) of leaf litter, dead wood, soil, and rocks in the dry season (Table 3). Grass cover decreased significantly from winter to summer (Paired T-test; $t = 11.6$; $p < 0.01$; Table 3). Forb cover increased significantly from winter to summer (Paired T-test; $t = 7.4$; $df = 11$; $p < 0.01$) with a significant increase in forb height (Paired T-test; $t = 4.71$; $df = 59$; $p < 0.01$; Table 3).

Table 3. The average (mean ± SD) ground cover (%) of grass, forbs, leaf litter, dead wood, rocks, and soil (n = 60 quadrats) in New Forest (*p < 0.05). Average grass and forb height (m) were compared between seasons (*p < 0.05).

	% Cover						Height (m)
	Grass*	Forbs*	Leaf litter*	Dead wood*	Rocks*	Soil*	Forb*
Winter	19.0 ± 25.9	18.6 ± 22.0	43.5 ± 24.3	9.7 ± 10.1	3.8 ± 9.2	5.2 ± 6.0	0.4 ± 0.3
Summer	0.1 ± 0.6	72.3 ± 24.0	18.5 ± 19.6	5.9 ± 6.0	1.3 ± 3.7	2.0 ± 4.0	0.7 ± 0.3

Only 23 bird species were observed in both winter and summer (Figure 3). Yellow-breasted Apalis *Apalis flavida* was the only species that foraged at the same height in both seasons (Figure 3). Ten species (44%) shifted < 2 m (five higher and five lower) but remained in the understory between seasons (Figure 3). The remaining 12 species shifted > 2 m where Greater Double-collared Sunbird *Cinnyris afer* showed the greatest shift (8 m) from the canopy in winter to the lower understory in summer (Figure 3). The majority (74%) of these species were insect-eaters (insectivores and omnivores). Unfortunately, statistical analyses could not test for significant differences due to low sample sizes in one season or another.

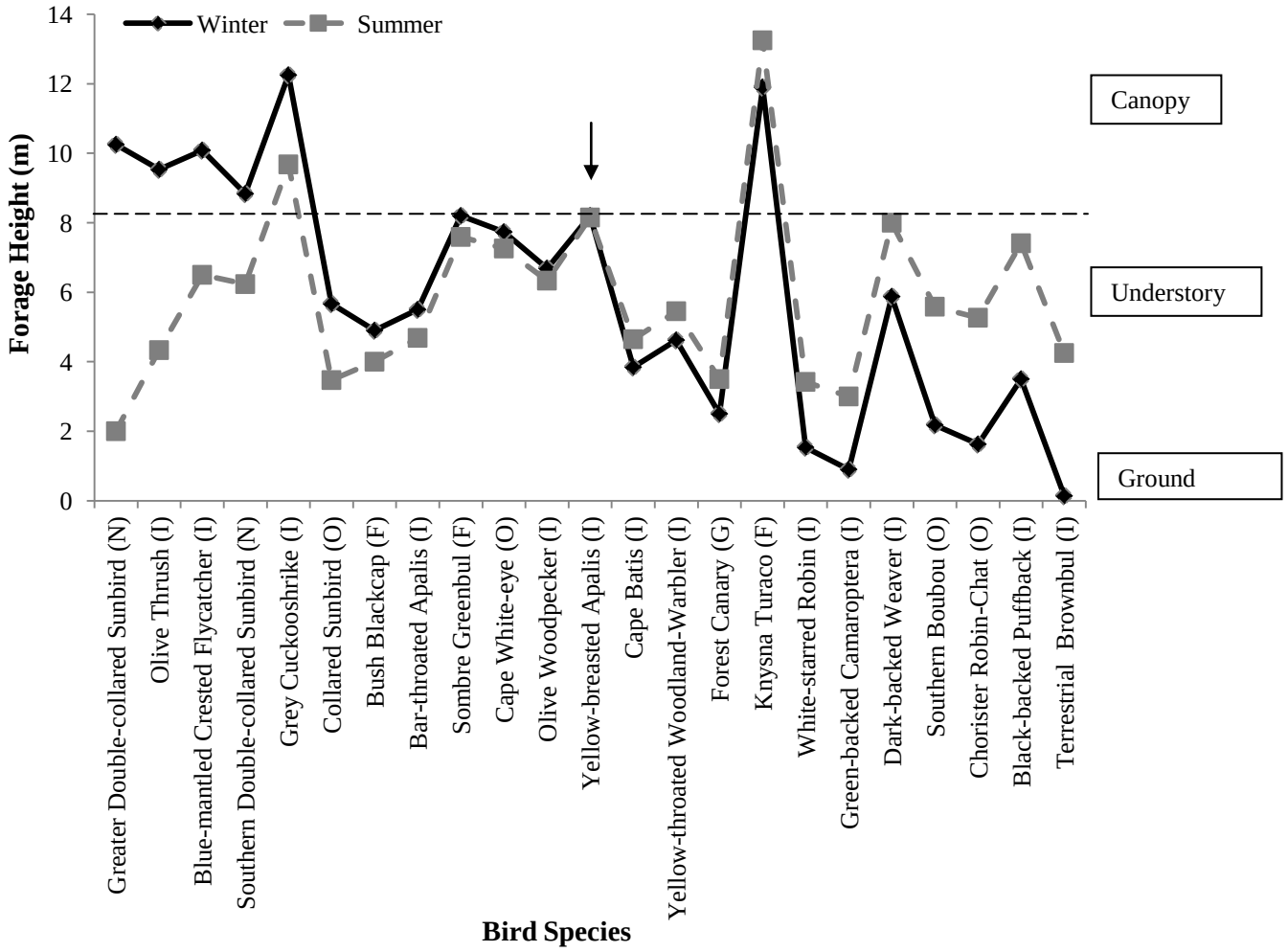

Figure 3. Mean forage height (m) of forest birds (n = 23) in winter and summer in New Forest, South Africa. Summer birds to the left of the arrow foraged in lower strata and birds to the right of the arrow foraged higher and *vice versa* for winter birds.

Insectivores and granivores were recorded foraging on the ground in winter but not in summer (Table 4). Frugivores exploited the abundant fruit in winter through a variety of manoeuvres, such as bite, hang, hover, and pluck (Table 4); but also foraged on invertebrates in both seasons. Nectarivores probed canopy flowers for nectar and used a variety of manoeuvres to obtain invertebrates in winter, but in summer were only recorded probing understory flowers (Table 4). The height at which nectarivores probed flowers decreased significantly from winter to summer (Mann-Whitney U Test: $Z = 3.2$; $p < 0.01$). Insectivores used several manoeuvres to obtain insects. Olive Thrush *Turdus olivaceus* also ate fruit from *Podocarpus latifolius* in winter. Many insectivores foraged higher in summer but the increase was only significant in hovering birds (Mann-Whitney U Test: $Z = 4.6$; $p < 0.01$; Table 4).

Table 4. The average (mean ± SD) forage height (m) at which a manoeuvre was employed (n = observations) per feeding guild, in winter (bold) and summer (italics) in New Forest (*p < 0.01).

	Insectivore (n = 16 spp.)	**Omnivore (n = 5 spp.)**	**Nectarivore (n = 4 spp.)**	**Frugivore (n = 4 spp.)**	**Granivore (n = 4 spp.)**	**Total**
Sift	**0.1 ± 0.2 (12)**	**1.0 ± 1.4 (2)**	-	-	**0.0 (1)**	**0.2 ± 0.5 (15)**
Peck	-	-	-	-	**0.3 (2)**	**0.4 ± 0.2 (5)**
Bite	-	-	-	**1.6 ± 0.4 (3)**	-	**1.6 ± 0.4 (3)**
Hang	-	-	-	**2.4 ± 1.1 (5)**	-	**2.4 ± 1.1 (5)**
	-	3.2 ± 0.9 (7)		-		3.2 ± 0.9 (8)
Hover	**2.5 ± 2.3 (18)***	**2.3 ± 1.4 (4)**	**4.0 (1)**	**11.0 (1)**	-	**2.9 ± 2.7 (24)**
	6.2 ± 2.8 (44)*	6.2 ± 3.9 (3)	-	2.0 (1)		6.1 ± 2.9 (48)
Glean	**4.4 ± 3 (55)**	**5.4 ± 3.9 (14)**	**8.7 ± 2.7 (6)**	-	-	**5 ± 3.3 (75)**
	5.5 ± 3.1 (48)	6.4 ± 3.6 (17)	-	8.5 (1)		5.8 ± 3.2 (66)
Hawk	**6.0 ± 1.2 (4)**	-	**10.0 ± 5.7 (2)**	**4.0 (1)**	-	**6.9 ± 3.4 (7)**
	9.1 ± 4.3 (7)	-	-	-		9.1 ± 4.3 (7)
Probe	**5.6 ± 5.4 (7)**	**5.3 ± 2.5 (12)**	**9.0 ± 4 (22)***	**11.5 (1)**	-	**7.4 ± 4.2 (42)**
	8.2 ± 4.3 (3)	3.0 (1)	3.4 ± 4.9 (10)*	-		4.4 ± 4.8 (14)
Pluck	**12.4 ± 1.7 (9)**	**6.3 ± 4.3 (4)**	-	**9.2 ± 5.5 (18)**	**7.2 ± 4.3 (12)**	**9.1 ± 4.8 (43)**
	-	3.5 (3)	-	13.5 ± 2.1 (2)		7.5 ± 5.6 (5)

3.4.2. Vertical stratification of food and feeding guilds

There was a close relationship between insectivore distribution and vegetation cover (Figure 4). The relative frequency of foraging insectivores increased in the upper strata with a significant increase in canopy cover from winter to summer, particularly within 2 - 5 m (Figure 4). In contrast, the proportion of foraging insectivores was significantly greater within 0 - 1 m in winter where vegetation cover was significantly lower than summer (Figure 4).

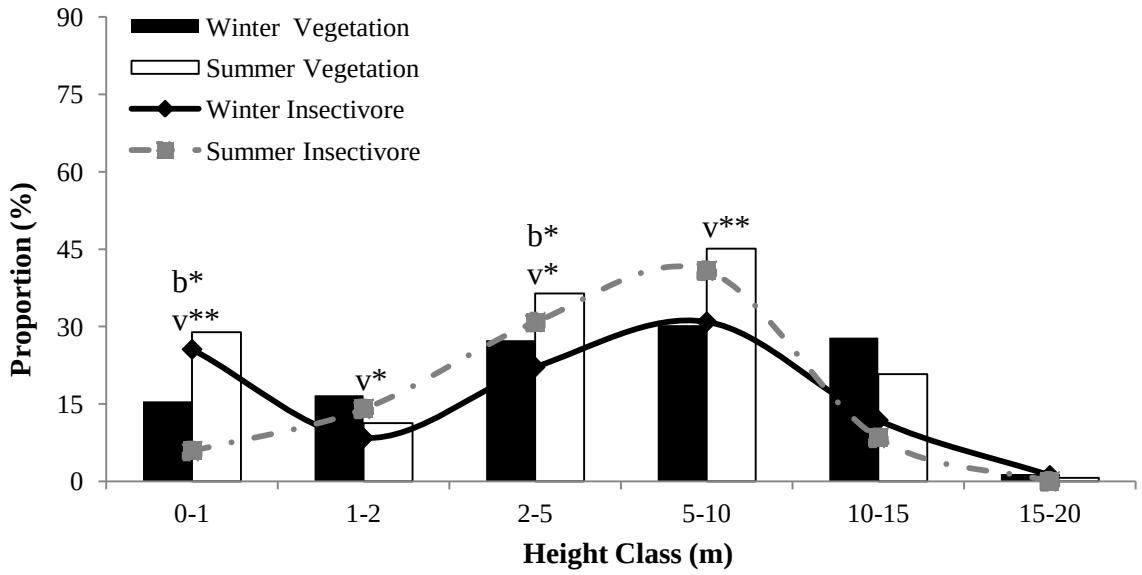

Figure 4. Relative frequency (%) of foraging insectivores (winter n = 13, summer n = 19 spp.) and vegetation cover (%) in winter and summer in New Forest. Vegetation cover and foraging birds increased between 2 - 10 m from winter to summer. An asterisk indicates a significant seasonal difference in vegetation (v) cover and bird (b) frequency (*p < 0.05; ** p < 0.01).

The greatest richness and abundance of invertebrates were collected on the ground in winter (75%) compared to the sticky traps and sweep nets (Kruskal-Wallis Test: $H = 36.8$, $p < 0.01$; Table 5). There was no significant difference between trap methods in summer (Table 5). A greater abundance of invertebrates were trapped with sweep nets and sticky traps in summer than winter, but this was only significant for sticky traps (Table 5).

Table 5. A comparison of total invertebrate abundance trapped with sticky traps, sweep nets, and pitfall traps between winter and summer (*p < 0.05). Species richness is in parentheses.

	Winter	Summer	Z	df	p
Order	16	18	-	-	-
Morphospecies	109	142	1.2	6	0.3
Sticky Trap Total	44 (18)	157 (16)	2.2	6	< 0.05*
Sticky Trap 3 m	21 (14)	52 (9)	2.2	6	< 0.05*
Sticky Trap 1m	23 (12)	105 (12)	2.2	6	< 0.05*
Sweep Net	228 (59)	441 (92)	0.9	6	0.4
Pitfall Trap	803 (62)	377 (86)	0.9	6	0.4
Total abundance	1075	975	0.3	6	0.8

Nectarivore foraging distribution was similar to the flower distribution (Figure 5). In winter, the majority of flowers (77%) were produced > 5 m (Sign Test: $Z = 1.2$; $p = 0.2$; $n = 3$) but in summer, all were produced < 5 m (Sign Test: $Z = 2.3$; $p < 0.05$; $n = 7$; Figure 5). The majority of fruit (77%; excluding fallen fruit on the ground) was produced > 5 m in winter (Sign Test: $Z = 3.5$; $p < 0.01$; $n = 47$), but in summer the majority of fruit (90%; excluding fallen fruit on the ground) was produced < 5 m (Sign Test: $Z = 8.7$; $p < 0.01$; $n = 92$; Figure 5). Omnivore distribution was similar to fruit distribution, particularly in summer but the majority of frugivores were recorded ≥ 5 m in both seasons (Figure 5). Unfortunately, statistical analyses could not be run because of low sample sizes in either food availability or birds in one season or another (Figure 5).

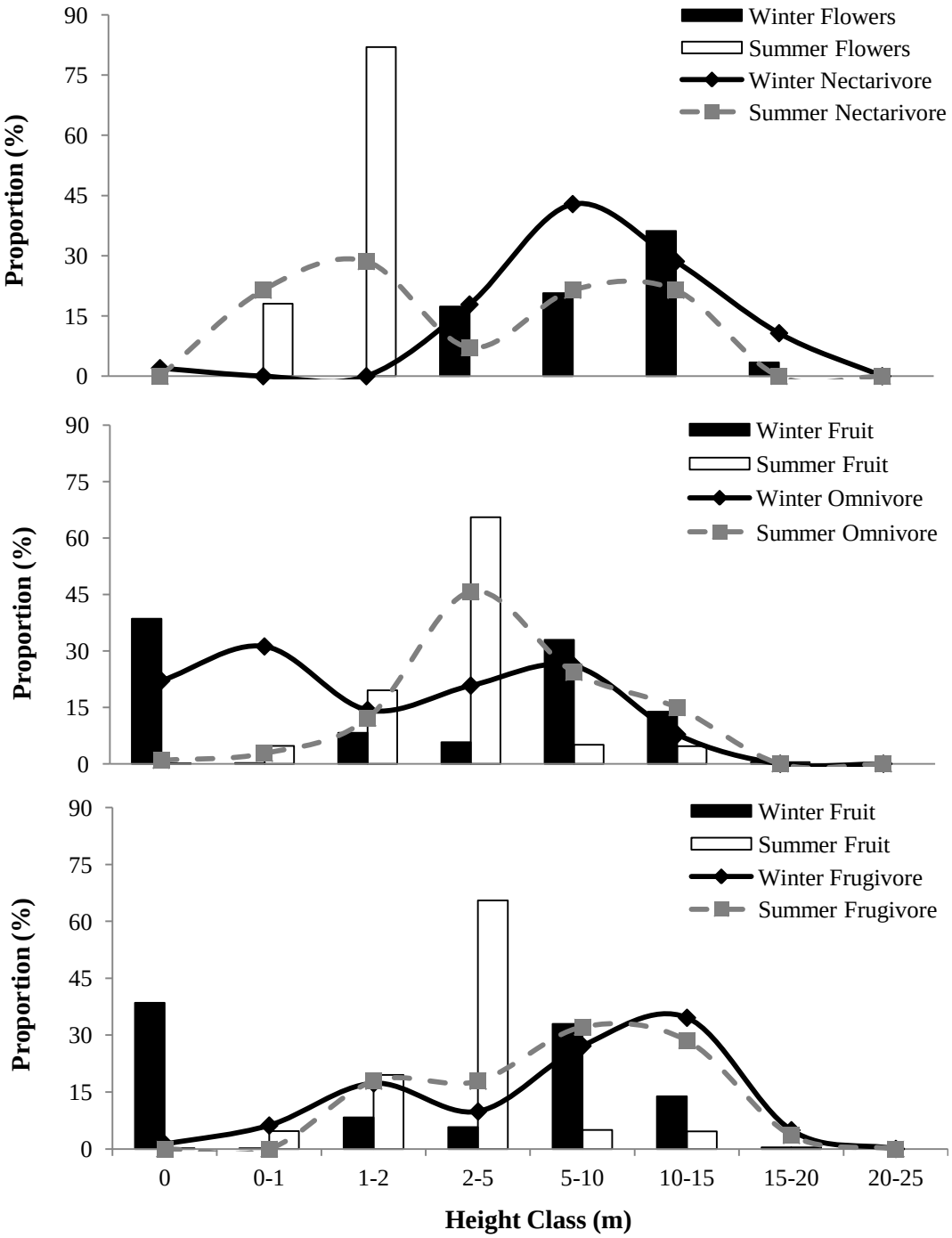

Figure 5. Relative abundance (%) of flower and fruit production (and fallen fruit) between winter and summer in New Forest. The relative frequency (%) of foraging nectarivores (winter n = 2 and summer n = 4 species), and omnivores (winter n = 5 and summer n = 4 species) are similar to the distribution of flowers and fruit respectively. Frugivores (winter n = 4 and summer n = 3 species) mostly foraged > 5 m.

3.4.3. Resource exploitation and differentiation

Intra-guild species target similar food resources but not all species obtain the resource in the same manner (Figure 6). Few intra-guild species used the same manoeuvre (or set of manoeuvres) to obtain prey (Figure 6). Congeneric species, like Chorister Robin-Chat *Cossypha dichroa* and Cape Robin-Chat *Cossypha caffra*, belonged to the same feeding guild but did not use the same manoeuvre to obtain prey (Figure 6). Nectarivores used a variety of manoeuvres to obtain insects in addition to nectar in the dry season but fed almost exclusively on nectar in summer (Figure 6).

Forest birds exploited 33 resource pools in winter but only exploited 15 pools in summer, almost half the number in winter. There was no apparent clustering between intra-guild species in winter but distinct clustering occurred in the insectivore and the nectarivore guilds in summer (Figure 7). There was little similarity between frugivores; particularly Bush Blackcap *Lioptilus nigricapillus* and Knysna Turaco *Tauraco corythaix* were different from all other guilds in either winter or summer (Figure 7). Species that are closer to one another have greater similarity than those that are further apart (StatSoft Inc 2012). In winter, the maximum forage range was 3 m by insectivores as opposed to a maximum range of 1 m by various guilds in summer (Figure 7).

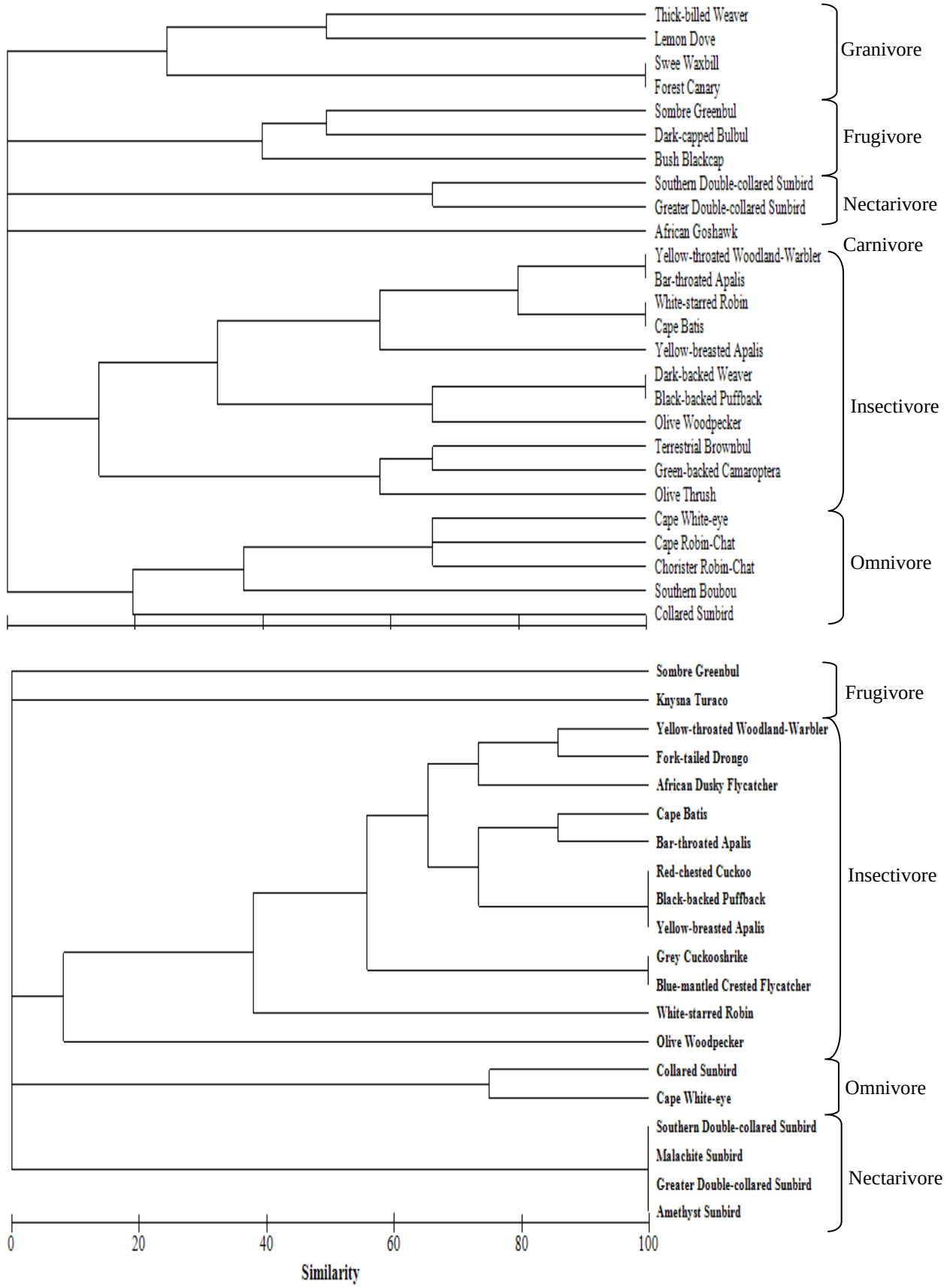

Figure 6. A dendrogram from a hierarchical cluster analysis based on Bray-Curtis similarity of manoeuvre employment between species in winter (above) and summer (below) in New Forest.

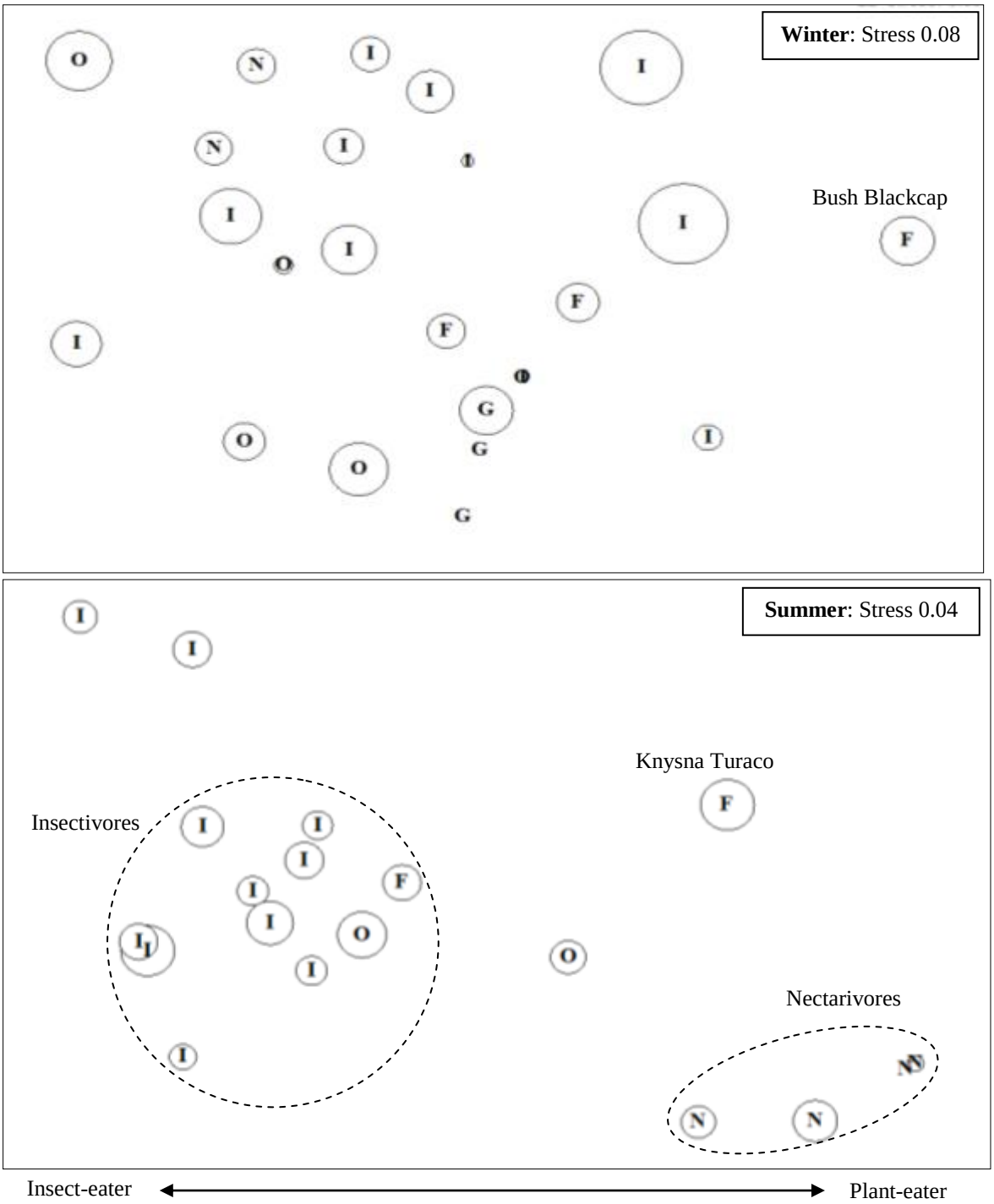

Figure 7. Forage niche differentiation in the winter and summer forest bird communities based on similarity in the average forage height (m) of pool exploitation (non-metric Multi-Dimensional Scaling bubble plot based on a Bray-Curtis similarity matrix in Primer 6.1.5.). Species are represented by their feeding guilds: insectivore (I), omnivore (O), nectarivore (N), frugivore (F), or granivore (G). Bubble size indicated the mean forage range per species from 0.1 to 3.0 m. Maximum forage range was 3 m in winter but 1 m in summer. The low stress values in both seasons indicated a high 'goodness-of-fit'.

3.5. Discussion

3.5.1. Vegetation structure and foraging birds

Forest composition and structure are important determinants of bird species presence and consequently diversity (MacArthur and MacArthur 1961; Diaz *et al.* 2005; Sallabanks *et al.* 2006). This is because composition determines food availability while structure influences the variety of forage substrates available to birds, which in turn determines bird foraging behaviour and success (Holmes *et al.* 1979; Maurer and Whitmore 1981; Robinson and Holmes 1984; Holmes and Robinson 1988; Downs and Symes 2004). Not all birds forage within the same strata because species are morphologically adapted to forage on particular substrates (Holmes *et al.* 1979). In addition, birds are not equally distributed along the strata but the canopy has a richer diversity of birds relative to the lower strata, particularly the ground (Pearson 1971; Bell 1982; Borghesio and Laiolo 2004). This study found that the greatest proportion of foraging birds was consistently recorded between 5 – 10 m in the higher strata, similar to Pearson (1971).

In summer, the proportion of foraging birds in the upper strata increased, where several of the ground-foraging birds moved from the ground into the upper strata. Some bird species were absent altogether. The reduction of ground-foraging birds may have been due to the increase in forb cover on the ground in summer. The dense herbaceous layer acts as an environmental 'barrier' to ground-foraging birds, reducing access to forage substrates, such as leaf litter, or reducing visibility of food resources, such as fallen fruit from trees like *Podocarpus latifolius*, *Scutia myrtina* and *Celtis africana*. The seeds and fruit are sources of high energy and if ground-foraging granivores like Thick-billed Weaver *Amblyospiza alifrons* and Lemon Dove *Aplopelia larvata*, and other birds, such as Olive Thrush *Turdus olivaceus* and do not have access to them, individuals will most likely leave the forest to where these resources are more accessible (Pearson 1971; also see Chapter 2). In addition, there was a significant increase in vegetation cover in the canopy due to the leafing of deciduous tree species, such as *C. africana* and *Dombeya* spp., in summer. The increase in leaf cover may have provided an additional food resource to invertebrates and therefore, a food source for foraging insectivores. Therefore, a seasonal change in vegetation cover has both direct and indirect effects on the vertical distribution of foraging birds.

3.5.2. Vertical stratification of food and feeding guilds

The nectarivores, Greater Double-collared Sunbird *Cinnyris afer* and Southern Double-collared Sunbird *Cinnyris chalybeus*, demonstrated the greatest shits in forage height from the canopy to lower strata from winter to summer. In winter, canopy trees like *Halleria lucida* were the dominant flowering plants while in summer *Sclerochiton odoratissimus* (shrub), *Scutia myrtina* (climber), and Red Hot Poker *Kniphofia* spp. (particularly towards the end of summer in the forest openings) were the most important flowering plants to birds (Chapter 2). Sunbirds tracked the vertical change in food because they are known to track abundant resources because they have a close relationship to their nectar resources (Fleming 1992; Craig and Hulley 1994; Borghesio and Laiolo 2004). The extent to which nectarivores exploit available resources not only depends on the spatial and temporal distribution of a resource but on the quality and quantity (Frost and Frost 1980). Although *H. lucida* is an abundant high quality nectar source to nectarivores (Frost and Frost 1980), sunbirds were observed foraging on invertebrates in winter. This was possibly due to a nitrogen limitation in the nectar or extra protein requirements in preparation for the breeding season (Fogden 1972; Wolf 1975; Wolf and Wolf 1976; Symes and Woodborne 2009). Although sunbirds are known to incorporate insects into their diet as well as nectar, sunbirds were observed foraging on invertebrates in winter but not in summer. This does not mean that the sunbirds never foraged on insects in summer, but possibly, they foraged on insects less frequently in summer than winter. Birds that had a close association with a food resource demonstrated a height shift in vertical distribution with a seasonal shift in food, and therefore the difference in forage height or range between species reflected food availability (Frith 1984; Holmes and Robinson 1988; Koen 1988; Borghesio and Laiolo 2004).

Gregarious frugivores also track food distribution over space and time (Levey 1988; Fleming 1992). However, in this study, individuals were most common in the canopy, regardless of the distinct shift in fruit abundance from the canopy to the understory from winter to summer. Omnivores, on the other hand, tracked the seasonal changes in fruit abundance, particularly in summer. Changes in invertebrate availability cannot be discounted, however, as some omnivores eat insects year round, whilst others only eat insects or plant material in a season depending on resource availability (Newton 2003; Borghesio and Laiolo 2004; Herrera *et al.* 2006). The greater abundance of invertebrates and fallen fruit on the ground in winter may have provided additional resources to ground-foraging omnivores. These resources were also more visible because of the high proportion of non-vegetated

ground in winter. However, the relative increase in invertebrate and fruit availability in the understory in summer may have driven the shift in forage height of these species from the ground into understory. Insectivores were most common in the canopy in both seasons but a high proportion of insectivores foraged on the ground in winter. Non-vegetated ground (with more exposed leaf litter and bare ground) together with an increase in invertebrate availability would have provided preferred conditions for ground-foraging insectivores, such as Terrestrial Brownbul *Phyllastrephus terrestris* that sifts through leaf litter, in winter. In contrast, other studies found an increase in the relative abundance of insectivores on the ground with the greatest increase of insectivores in the understory in the wet season (Borghesio and Laiolo 2004).

Many of the foraging heights are within the same range as observed in the Knysna forests in South Africa (Koen 1988). However, compared with Koen (1988), the data in this study were not combined, so that seasonal comparisons could be made. Overall, this study found a vertical shift in the foraging distribution of nectarivores, omnivores, and insectivores in response to a vertical shift in food abundance, and to some extent, a change in vegetation structure. Moreover, the seasonal shift in the vertical distribution of sunbirds in response to changes in flower availability and the lack of vertical shift in frugivorous species (the prominence of frugivores in the canopy in both seasons) is similar to studies done in other forests (Pearson 1971; Bell 1982; Koen 1988; Borghesio and Laiolo 2004). Bird species that did not shift in forage height may be specialist to a certain stratum, such as a strict canopy frugivore like the Knysna Turaco *Tauraco corythaix* (Koen 1988).

3.5.3. Resource exploitation and differentiation

A feeding guild comprises several species that compete for a similar food resource in a similar manner (Root 1967). Assuming that all bird species that have been outcompeted in the past are no longer present in the forest, the remaining species will co-exist so that a desired resource is obtained maximally with minimum conflict (Wiens 1989). Intra-guild species divide food to avoid competition using a different manoeuvre or set of manoeuvres from a competitor (Koen 1988). For example, species, such as Olive Woodpecker *Dendropicos griseocephalus* that probe tree bark for grubs will exploit a different sub-set of the insect resource from a bird, such as Cape Batis *Batis capensis*, that gleans insects like caterpillars from leaves. Therefore, although these two species are insectivores, competition is avoided through the employment of a particular manoeuvre or a different set of

manoeuvres. Phylogenetically similar species do not always exploit the same set of resources (Simberloff and Dayan 1991; Wilson 1999). However, congeneric species, such as Bar-throated Apalis *Apalis thoracica* and Yellow-breasted Apalis *Apalis flavida* that both target insects and are similar in mass and other morphological and biological traits (Hockey *et al.* 2005) will compete for food. This study indicated that congenerics did not acquire resources in the same manner in either season, indicating differences in the exploitation of insects and therefore minimised conflict. In the dry season, few intra-guild species used the same set of manoeuvres to capture their prey, but in summer, similarity increased, particularly within the insectivore and nectarivore guilds. Competition for a desired resource, therefore, appeared to intensify in winter when resources were limited. Therefore, the increased segregation in resource selection in winter may have been to reduce the potential for inter-specific competition, particularly intra-guild species (Alatalo 1982).

Birds do not only differ in manoeuvre from a competitor but also forage on different substrates or at different heights from one another (Alatalo 1982; Sabo and Holmes 1983; Frith 1984; Ford *et al.* 1986; Koen 1988). The differential use in forage height and forage site is considered some of the most important factors in niche differentiation between species for competition avoidance (Alatalo 1982; Sabo and Holmes 1983; Frith 1984). Each variable can be considered as a 'pool' that provides a sub-set of resources to an individual, and therefore the sum of the set of environmental pools that an individual exploits can be defined as its foraging niche in this study. In winter, there was low similarity in pool exploitation between bird species. There was also a weak division of insect-eaters from plant-eaters (fruit-, seed- and nectar-feeding species). Nectarivores, for example, foraged on invertebrates in winter and therefore exploited a similar niche to insect-eaters, in at least one dimension. In summer, however, there was greater similarity between intra-guild bird species as individuals were more selective in pool exploitation. The number of exploited pools halved from winter to summer (33 pools in winter and 15 pools in summer) and distinct groups of feeding guilds formed, such as the insectivore-cluster and the nectarivore-cluster. This may have been because preferred resources were more readily available in the wet season than in the dry season. Consequently, there was a greater overlap in intra-guild bird species where species exploited resources at similar foraging heights and substrates. Therefore, unlike a similar study in the Afromontane forests of Kenya that did not find discernible shifts in foraging ecology between seasons (Borghesio and Laiolo 2004), this study showed that there were shifts in pool exploitation between the dry and wet seasons, particularly within guilds. This

may have been due to a seasonal change in both food and substrate availability which have been shown to affect guilds differently.

Dissimilarity in manoeuvre selection between species is not necessarily indicative of low resource abundance. There was a higher abundance and variety of fruit in winter than summer because *Podocarpus latifolius* and *Celtis africana* provided mass food contribution to forest birds (Chapter 2). In addition, fruit diversity was high due to the high number of plant species fruiting in the dry season. Several different types of manoeuvres were employed by various frugivores in which to exploit the different types of fruit. Therefore, low niche similarity between these species may have been because there was an increased variety of fruit available in winter than summer, rather than the fact that this resource was limiting. Although some frugivores like the Knysna Turaco is considered a specialist, most frugivores behave as generalist-feeders and closely adjust their diet to the seasonal abundance of a food-type (Cotton 1996). For example, many frugivores also incorporate invertebrates in their diet, because fruits are low in protein and lipids (Fogden 1972), and the proportion of insects in the diet varies between seasons. Sombre Greenbul *Andropadus importunus*, for example, had a mixed diet of fruit and invertebrates in winter but was only observed eating insects in summer. Many frugivores left the forest in summer when fruit diversity and abundance decreased (Chapter 2).

Winter birds foraged over a broader height range than summer birds. Consistent with other studies, the majority of species that foraged over the broadest vertical range in both seasons were insect-eaters possibly due to an increased diversity of invertebrate availability (Frith 1984; Koen 1988). Similarly, birds in the Knysna forest of South Africa were also considered to be patch generalists as many species foraged broadly over the strata in search of food; however these results were based on combined data over a year and not between seasons where resources may be more limiting in one season compared to another (Koen 1988). Therefore, in the dry season niche width increased for several species, but no niche was so similar that there was high overlap between any species. This implies that resources were limited (either in quality or quantity) in the dry season and so the number of exploited pools increased in addition to forage range. Consequently, when resources are scarce individuals cannot preferentially forage on a preferred resource (Alatalo 1982), and therefore, many bird species become generalists in both food and substrate selection. Birds therefore expand and contract their vertical forage range seasonally in search of food (Pearson 1971).

3.6. Conclusion

Seasonal food abundance drives the foraging ecology of birds. Food limitation within a season is species- and guild-dependent. Niche overlap is determined by niche width, which in turn is influenced by, 1) structural changes in the vertical profile of vegetation, 2) quantitative changes in food, and 3) qualitative changes in available food. Nectarivores, omnivores, and insectivores have a close association with their food source and tracked food abundance along the vertical strata. Insectivore foraging distribution was also influenced by seasonal variation in forage substrate. There was a higher level of resource partitioning between birds in winter, and birds exploited a higher number of resource pools and foraged over a broader vertical range. Therefore, niche separation was higher between birds in the dry season when food was limiting, as opposed to summer when food was abundant. The increase in niche breadth in response to resource limitation followed the predictions of the optimal foraging niche theory (Pyke *et al.* 1977); where a broader niche maximises the return per unit of forage effort (Koen 1988).

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3.9. Appendix 1

The number of foraging observations for forest birds recorded in winter (W, July/August 2010) and summer (S, January/February 2011) in New Forest, KwaZulu-Natal. The feeding guild (FG), average forage height (m, FH), manoeuvre employed (M), and the number of exploited resource pools (RP) are also given. Feeding guilds include carnivore (C), insectivore (I), omnivore (O), nectarivore (N), frugivore (F), and granivore (G). Manoeuvres include sift (a), pounce (b), peck (c), bite (d), hover (e), hang (f), hawk (g), probe (h), pluck (i), glean (j), not observed (NO).

Bird species	FG	W	S	WFH	SFH	WM	SM	WRP	SRP
African Goshawk *Accipiter tachiro*	C	1	-	0	-	b	-	1	-
Lemon Dove *Aplopelia larvata*	G	2	-	0	-	c	-	1	-
Knysna Turaco *Tauraco corythaix*	F	5	4	11.9 ± 1.4	13.3 ± 1.3	-	i	-	1
Red-chested Cuckoo *Cuculus solitarius*	I	-	2	-	5.8 ± 1.1	-	ej	-	2
Narina Trogon *Apaloderma narina*	I	-	1	-	4.0	-	-	-	-
Olive Woodpecker *Dendropicos griseocephalus*	I	4	3	6.7 ± 7.0	6.3 ± 2.1	h	h	2	1
Grey Cuckooshrike *Coracina caesia*	I	2	14	12.3	9.7	-	e	-	1
Fork-tailed Drongo *Dicrurus adsimilis*	I	-	7	-	9.1 ± 3.8	-	egj	-	4
Southern Black Tit *Parus niger*	I	-	1	-	12.0	-	-	-	-
Bush Blackcap *Lioptilus nigricapillus*	F	5	2	4.9 ± 4.3	4.0	i	-	1	-
Dark-capped Bulbul *Pycnonotus tricolor*	F	16	-	9.4 ± 3.8	-	efgi	-	4	-
Terrestrial Brownbul *Phyllastrephus terrestris*	I	8	2	0.1 ± 0.2	4.3	a	-	1	-
Sombre Greenbul *Andropadus importunus*	F	19	11	8.2 ± 6.9	7.6 ± 4.4	dfic	ej	5	2
Olive Thrush *Turdus olivaceus*	I	16	3	9.5 ± 5.1	4.3 ± 7.5	ai	-	2	-
Chorister Robin-Chat *Cossypha dichroa*	O	12	3	1.6 ± 3.3	5.3 ± 5.0	aij	-	3	-
Cape Robin-Chat *Cossypha caffra*	O	14	-	1.3 ± 1.2	-	acehij	-	5	-

Bird species	FG	W	S	WFH	SFH	WM	SM	WRP	SRP
White-starred Robin *Pogonocichla stellata*	I	21	8	1.5 ± 2.2	3.4 ± 2.7	egj	j	5	1
Yellow-throated Woodland-Warbler *Phylloscopus ruficapilla*	I	29	54	4.6 ± 3.3	5.5 ± 2.5	ej	efgj	4	5
Bar-throated Apalis *Apalis thoracica*	I	27	31	5.5 ± 4.1	4.7 ± 3.6	ej	ehj	7	4
Yellow-breasted Apalis *Apalis flavida*	I	15	10	8.2 ± 3.3	8.2 ± 4.1	j	ej	1	2
Green-backed Camaroptera *Camaroptera brachyura*	I	4	1	0.9 ± 1.7	3.0	aj	-	3	-
African Dusky Flycatcher *Muscicapa adusta*	I	-	4	-	6.6 ± 4.3	-	eg	-	2
Cape Batis *Batis capensis*	I	34	56	3.8 ± 2.7	4.6 ± 2.6	egj	eghj	8	5
Blue-mantled Crested Flycatcher *Trochocercus cyanomelas*	I	6	3	10.1 ± 2.7	6.5 ± 1.7	-	e	-	1
African Paradise-Flycatcher *Terpsiphone viridis*	I	-	4	-	8.1 ± 3.7	-	-	-	-
Southern Boubou *Laniarius ferrugineus*	O	14	3	2.2 ± 1.8	5.6 ± 3.2	egj	-	4	-
Black-backed Puffback *Dryoscopus cubla*	I	7	11	3.5 ± 1.9	7.4 ± 1.6	hj	ej	3	3
Olive Bush-Shrike *Telophorus olivaceus*	I	1	-	12.0	-	-	-	-	-
Southern Double-collared Sunbird *Cinnyris chalybeus*	N	30	6	8.8 ± 3.9	6.2 ± 6.1	eghj	h	5	1
Greater Double-collared Sunbird *Cinnyris afer*	N	2	4	10.3	2.0 ± 0.7	hj	h	2	1
Amethyst Sunbird *Chalcomitra amethystina*	N	-	1	-	0.8	-	h	-	1
Collared Sunbird *Hedydipna collaris*	O	9	17	5.7 ± 2.2	3.5 ± 0.9	h	fhij	2	4
Cape White-eye *Zosterops virens*	O	15	33	7.7 ± 2.8	7.3 ± 3.9	hij	efij	6	5
Thick-billed Weaver *Amblyospiza albifrons*	G	14	-	6.2 ± 4.8	-	-	-	3	-
Dark-backed Weaver *Ploceus bicolor*	I	4	1	5.9 ± 3.2	8.0	hj	-	3	-
Swee Waxbill *Coccopygia melanotis*	G	1	-	5.0	-	-	-	1	-
Forest Canary *Crithagra scotops*	G	2	4	2.5	3.5 ± 4.3	i	-	1	-

Chapter 4: Seasonal dietary shifts in forest birds

Artist: Veronica Herbert

Seasonal changes in the dietary patterns of forest birds

Samantha L. Scott [1]*, Craig T. Symes [1], Stephan M. Woodborne [2], and Andrew E. McKechnie [3]

[1] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, P/Bag 3, Wits 2050, South Africa

[2] Natural Resources and the Environment, Council for Scientific and Industrial Research, P.O. Box 395, Pretoria 0001, South Africa

[3] DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

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***Corresponding author:**

Samantha L. Scott
School of Animal, Plant and Environmental Sciences
University of the Witwatersrand
Private Bag 3
Wits, 2050
South Africa
Email: samantha.scott@students.wits.ac.za
Telephone: +27 (0)11 717-6478
Facsimile: +27 (0)11 717-6494

4.1. Abstract

Stable carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope analysis was used to assess seasonal shifts in dietary source and trophic structure of a forest bird community between winter and summer. Data were collected from an Afromontane forest patch in KwaZulu-Natal, South Africa. Plant material was collected from the forest and surrounding grassland. Invertebrates were sampled using the pitfall trap and sweep net methods, and whole blood was drawn from birds captured with mist nets and baited flap traps in the forest. Forest birds were classified as forest specialists, forest generalists, and forest visitors to gain further insight into the dietary patterns of forest birds between seasons. In winter, birds appeared to forage on similar food sources, but in summer, there was discrete isotopic clustering in forest specialists and generalists as well as in forest edge species. Most forest birds had a high proportion of C_3 in their diet, particularly the forest specialists and generalists, but the proportion of dietary C_3 decreased in summer for most species. There were trophic level shifts in some forest birds from winter to summer due to changes in the quantity and quality of food in the system, but these changes were species-specific. These patterns suggest that forest birds are generalist feeders in winter but select preferred food resources in summer, possibly because food resources were quantitatively, and in some cases qualitatively, limited in winter but not in summer. Several studies pool isotopic data collected over several months but we recommend that seasons are analysed separately for further insight into the dietary patterns of forest birds.

Keywords: Carbon and nitrogen stable isotopes, isotopic community, forest dependency, dietary shifts

4.2. Introduction

Forests are recognisable ecosystems that support unique floral and faunal species (Castley and Kerley 1996). However, forests systems are globally threatened because of human disturbances, such as deforestation and exploitation of forest products for medicinal purposes (Pomeroy and Service 1992; Castley and Kerley 1996; Crawley 2003; Neuschulz *et al.* 2011). Sub-tropical forest is the smallest and most widely dispersed biome in southern Africa, and differs from tropical forest in that they are naturally fragmented (Geldenhuys and MacDevette 1989; Eeley *et al.* 2001). Patches are surrounded by a non-forest matrix, generally grassland (White 1981; Mucina and Geldenhuys 2006). Anthropogenic disturbance

has contributed to the decline of indigenous forest in southern Africa where some patches have disappeared altogether (Geldenhuys and MacDevette 1989; Eeley *et al.* 1999; Kotze and Samways 1999; Lawes and Eeley 2000), and many of the remaining patches will continue to be harvested unsustainably for forest products (Eeley *et al.* 1999). Forests contain a large proportion (14%) of terrestrial bird species in southern Africa (Geldenhuys and MacDevette 1989) and are well represented in conserved areas (Geldenhuys and MacDevette 1989; Eeley *et al.* 1999). However, processes that determine community structure are not well understood, which makes forest management and conservation difficult (Lawes *et al.* 2000).

Food is one of the most important limiting resources to terrestrial birds (Elton 1927; Lack 1968; Holmes *et al.* 1979), and therefore an important driver in bird community structure. Communities form because species are able to co-exist in an ecosystem due to the partitioning of resources (Elton 1927; Schoener 1974). Basal food resources, predation, and competition for resources determine trophic structure (Leibold *et al.* 1997) where the feeding relationships between species together with energetic constraints separate species into different trophic levels (Elton 1927; Leibold *et al.* 1997). Food production, however, is stochastic. Forests, for example, produce a variety of food resources that fluctuate over space and time (Hopkins 1977; Herrera *et al.* 2003; Herrera *et al.* 2005; Mucina and Geldenhuys 2006). Southern African forests are similar to tropical forests in that there is an irregular and highly variable intra- and inter-seasonal fruiting and flowering phenology (Liversidge 1972; Koen 1992; Wirminghaus *et al.* 2001). Numerous plants in tropical forests flower or fruit in the dry season but wind- and insect-pollinated flowers are produced in the wet season (Koen 1992; Murali and Sukumar 1994; Mac Nally and McGoldrick 1994; Borghesio and Laiolo 2004). The seasonal and spatial variation of food availability in forest systems, in either quantity or quality, influences a bird's ability to meet individual food requirements (Hopkins 1977; Herrera *et al.* 2003; Mucina and Geldenhuys 2006). Some bird species, for example, track food to areas of increased periodic abundance while resident species modify their diet or diet-switch completely depending on the dominant food-type available (Fleming 1992; Koen 1992).

Certain bird species are important and useful indicators of forest condition (Bennun *et al.* 1996; Lawes *et al.* 2000). Birds that are particularly dependent on relatively intact, undisturbed forest are of particular conservation concern (Bennun *et al.* 1996). Forest specialists are dependent on the forest for reproduction, forage, and survival, and do not move readily between patches (Oatley 1989; Bennun *et al.* 1996). These species are less adaptable than other forest-utilising species, are of relatively limited distribution, and are

unlikely to disperse through, or utilise, non-forest habitat, and are most likely to disappear when forests are extensively modified (Bennun *et al.* 1996; Neuschulz *et al.* 2011). Forest specialists, therefore, are of greatest conservation concern (Bennun *et al.* 1996). However, bird species differ in the degree of dependency and a large proportion of forest birds are not restricted to the forest environment (Geldenhuys and MacDevette 1989). Forest generalists partly rely on forest for their survival but are common in non-forest environments like savanna woodland. Forest visitors on the other hand, are birds that are not dependent on the forest for survival and more likely to occur in other vegetation-types (Bennun *et al.* 1996). The forest specialists, and to some extent forest generalists, are important to identify as they are less widespread and more susceptible to human disturbance and therefore most vulnerable to changes in forest composition and physiognomy than are forest visitors (Bennun *et al.* 1996; Neuschulz *et al.* 2011).

Stable light isotope analysis, particularly of carbon and nitrogen, in combination with conventional methods, has become an important and powerful tool in the identification of habitat and food selection as well as dietary range of birds from the individual to community level (see Inger and Bearhop 2008 for review; Newsome *et al.* 2012). Forest plants are C_3-dominated while grasslands are predominantly C_4 (Peterson and Fry 1987; Ehleringer and Cerling 2002; Bond and Parr 2010). Crassulacean Acid metabolism (CAM) plants have a similar isotopic value to C_4 (Smith and Epstein 1971). C_4/ CAM plants also grow in the forest but are not as common C_3 plants, and *vice versa* in the grassland. The carbon isotopic signatures differ between plants where C_3 plants have a typical depleted $\delta^{13}C$ value of *c.* -28‰ but C_4 grasses have an enriched $\delta^{13}C$ value of *c.* -13‰ because of the different photosynthetic pathways (Smith and Epstein 1971; Peterson and Fry 1987; Hobson and Clark 1992a). Much of the variation in $\delta^{13}C$ in birds is ascribed to the differential use of C_3 and C_4 plants between the forest and grassland (Peterson and Fry 1987). Therefore, the level of forest dependency between strict forest birds and other forest-associated species can be identified because the isotopic signature of bird tissues, regardless of trophic level, reflects the dietary source in a predictable way (Bearhop *et al.* 2002; Inger and Bearhop 2008; Prochazka 2010). This is because carbon fractionates relatively little (between 0 - 1‰) per trophic level increase and the trophic level of an organism determines the $\delta^{15}N$ signature of its tissues relative to the basal nitrogen source from plants in a system, with a 2 - 4‰ increase per trophic level (Post 2002; Inger and Bearhop 2008). Nitrogen, in particular, reflects temporal dietary shifts, such as diet-switching, in some species (Inger and Bearhop 2008).

The dual approach of carbon and nitrogen isotopic analysis provides insight into both the basal dietary source as well as the trophic structure within bird communities (Post 2002; Herrera *et al.* 2003; Inger and Bearhop 2008; Prochazka 2010). Therefore, the aim of this study was to assess the seasonal dietary patterns of bird species within an Afromontane forest bird community between winter and summer. Stable light isotope analysis of carbon and nitrogen was used to assess, 1) the dietary source to forest birds, particularly between forest specialists, forest generalists, and forest visitors, and 2) the seasonal dietary shifts and trophic level shifts within species.

4.3. Methods

4.3.1. Site description

Research was conducted on the privately owned New Forest Farm (29°27'53"S 29°52'54"E), a 112 ha forest patch (Cooper 1985) surrounded by montane grassland, located 1 380 - 1 740 m above sea level in KwaZulu-Natal, South Africa (Figure 1). New Forest is an Afromontane Mist Belt Mixed *Podocarpus* Forest in the Southern Mist Belt Forest region. The forest patch comprises tall evergreen and deciduous trees (*c.* 15 - 20 m) and is multilayered with a dense understory and a well-developed herbaceous layer on the forest floor (Mucina and Geldenhuys 2006). Dominant trees in the canopy include *Podocarpus latifolius*, *Celtis africana,* and *Halleria lucida*. Several natural openings in the forest host a dense layer of wetland species, such as *Cyperus* and *Kniphofia* spp. enclosed by stands of *Leucosidea sericea*. The area receives *c.* 1 000 mm annual rainfall. Winter (June to August) receives < 50 mm rainfall per month while summer (December to February) receives > 100 mm per month with frequent mist, which supplements rainfall considerably (Mucina and Geldenhuys 2006). Isotope samples were collected during winter (14 to 24 August 2010) and summer (17 to 24 January and 22 to 25 February 2011). As blood primarily reflects dietary protein within the past 3 weeks of capture (Bearhop *et al.* 2002), birds were captured at the end of each season to obtain isotopic information regarding food assimilation.

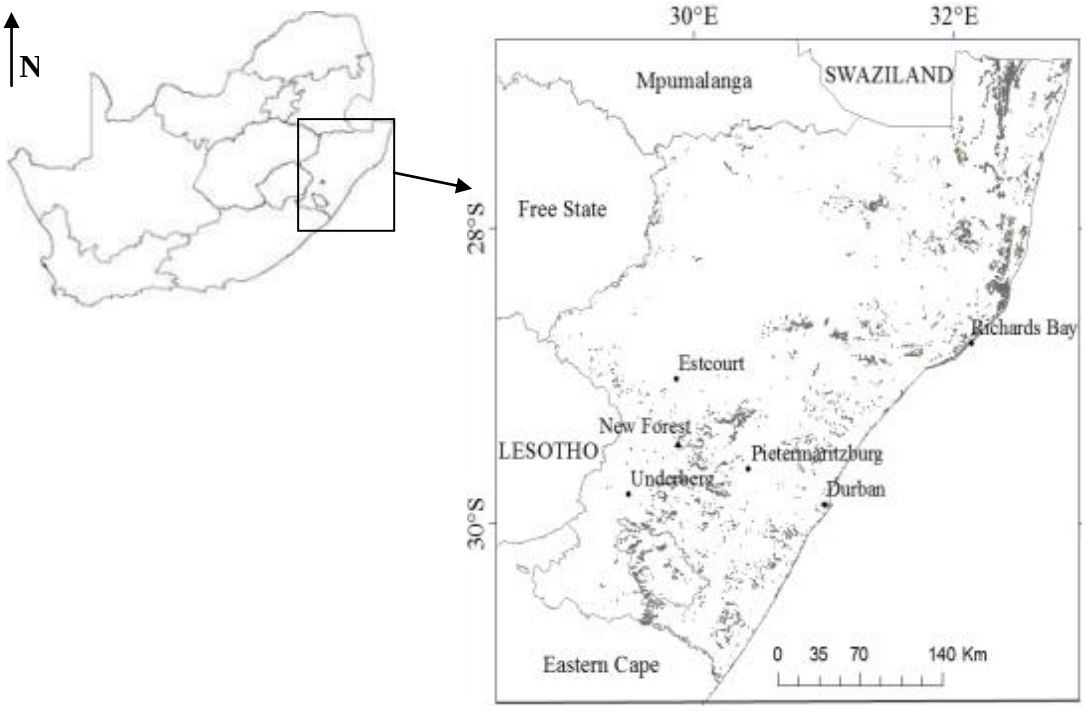

Figure 1. Mosaic of natural forest (grey shading) and grassland in KwaZulu-Natal (*source:* South African Department of Agriculture, Fisheries and Forestry). New Forest (triangle) and selected towns (dots) are plotted for reference purposes. Inset: Map of South Africa with the location of New Forest (triangle).

4.3.2. Fieldwork

4.3.2.1. Invertebrate sampling

Invertebrate sampling took place over three days using pitfall traps and sweep nets within six 400 m^2 quadrats per season. Five pit fall traps (white plastic cups 108 mm in diameter and 60 mm deep) were buried ≥ 5 m apart, with the brim at ground level (n = 30 per season). The traps were filled with a non-toxic surfactant solution (1 drop dishwashing liquid per 1 L tap water) to ensure the entrapment of invertebrates. Sweep netting was done for five minutes per day (*c.* 30 - 50 sweeps per minute depending on openness of vegetation) within the lower 2 m of the forest, which was enough time to sample the entire quadrat. All collected invertebrates were stored in 75% alcohol. In the laboratory, the invertebrates were categorized into morphospecies based on physical attributes and placed on glass petri dishes to evaporate the alcohol before isotopic analysis. Whole invertebrate samples were used as whole specimens are usually ingested by birds.

4.3.2.2. Plant sampling

Plant material including leaves, fruit, and flowers was collected within the lower 2 m of the forest strata and as well as from the surrounding grassland. Samples represented C_3 and C_4 end-points against which dietary associations and comparisons could be made (Symes and Woodborne 2009). Dry plant material was stored in brown envelopes and fruit was stored in 75% alcohol until analysis. In the laboratory, the alcohol on the fruit material was poured off and the remaining material was dried to a constant mass at 70 ˚C. Plant fragments were treated with 1% HCl for *c.* 24 hours to remove carbonates, rinsed with distilled water to pH 5, and then dried to a constant mass at 70 ˚C. Dried samples were ground to a homogeneous powder using a ceramic mortar and pestle and stored in labelled Eppendorf (R) containers until isotope analysis.

4.3.2.3. Bird sampling

Understory forest birds were caught with nylon mist-nets (10-12 m X 3 m X 16 mm mesh; Safring, Cape Town). Nets were set up along forest trails and established paths leading from the edge into the forest interior, using 3 m aluminium poles. Sampling occurred from dawn to dusk and nets were checked every 15 - 30 minutes over a period of 10 days per season. All birds were ringed to prevent re-sampling the same individual. Ground-foraging birds were caught using flap traps baited with mealworms (*Tenebrio* spp.) in both the forest and grassland. Most of the birds defecated during handling and the faecal samples were retained for isotope analysis. Preparation of faecal samples for isotopic analysis followed the same protocol used for plant material. Approximately 75 µL blood samples were drawn from the brachial vein of each individual, dried at 70 °C until constant mass, and then stored at *c.* 7 °C until isotope analysis.

4.3.3. Laboratory analysis

Isotopic analyses were run on a DeltaV Advantage Stable Light Isotope Mass Spectrometer coupled to a Flash EA, 1112 Elemental Analyser using a ConfloIV interface (all instrumentation supplied Thermo Fisher Scientific, Bremen, Germany). For solid samples (plant material, faecal matter, and invertebrates) approximately 1 mg (where sufficient material was available) duplicate aliquots were weighed into pre-cleaned tin cups. Blood samples were analysed using the protocol of Symes *et al.* (2011). On-line combustion took place at 1020 °C. A calibrated laboratory standard (Merck gel) and blank were analysed after

12 unknowns in a run. Isotope ratios are expressed relative to Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen in δ notation (parts per thousand; ‰) using the following equation:

$$\delta^{15}X = [(R_{sample} - R_{standard}) - 1] \times 1000 \quad (1)$$

where X is the element of interest and R is the corresponding ratio of $^{15}N:^{14}N$ or $^{13}C:^{12}C$. Typical precision of an internal standard was *c.* 0.3‰ for carbon and *c.* 0.1‰ for nitrogen in winter and *c.* 0.1‰ for carbon and *c.* 0.3‰ for nitrogen in summer.

4.3.4. Data analysis

All data were tested for normality with a Kolmogorov-Smirnov test prior to statistical analyses, and all statistical analyses were done in Statistica 6.1.478.0 (Statsoft. Inc. 2004). All results are presented as mean ± SD. An Independent T-test was used to compare the $\delta^{15}N$ signatures of bird whole blood and invertebrate material between winter and summer. A Mann-Whitney U Test was used to test for a significant difference in the $\delta^{15}N$ signatures of C_3 fruit between seasons as well as in carbon contribution between the two forest bird communities. Inter-specific variation in both $\delta^{13}C$ and $\delta^{15}N$ within the forest bird community was tested using a Kruskal-Wallis Test whereby only species with a sample size > 2 were considered. A linear regression at a 95% confidence interval was used to test the relationship between $\delta^{13}C$ and $\delta^{15}N$ in each forest bird community. However, a Spearman Rank Correlation was used to test for a relationship between $\delta^{13}C$ and $\delta^{15}N$ in forest specialists, generalists, and visitors. However, grassland birds with $\delta^{15}N > -19‰$ were excluded as these values may skew results of the actual forest community. Trophic levels were calculated according to the equation:

$$TL_{consumer} = 1 + [(\delta^{15}N_{consumer} - \delta^{15}N_{producer})/3.1] \quad (2)$$

where $TL_{consumer}$ is the trophic level of the organism, $\delta^{15}N_{producer}$ is equal to the average $\delta^{15}N$ value of C_3 plants in New Forest per season and 3.1 the average discrimination factor of winter (2.9 ± 1.4) and summer (3.3 ± 1.2) combined. The average diet-tissue discrimination factor was the same value calculated in other studies (Hobson and Clark 1992b; Herrera *et al.* 2003) and was determined from the following equation (Vanderklift and Ponsard 2003):

$$\Delta = ‰^{15}N_{consumer} - ‰^{15}N_{diet} \quad (3)$$

where 'diet' is the isotopic signature of faecal matter. All faecal matter was rinsed before isotope analysis, which removed the urinary component. Therefore, the faecal material without the urea is isotopically similar to, and represents, ingested material.

4.4. Results

4.4.1. Isotopic community structure and the food base

There was a slight, yet non-significant, enrichment of $\delta^{15}N$ in C_3 plants (excluding C_3 fruit) from winter (-0.04 ± 2.2‰; n = 19) to summer (0.02 ± 0.5‰; n = 24) but there was a significant depletion in $\delta^{15}N$ of C_3 fruit from winter to summer (Mann-Whitney U: Z = 3.9, $p < 0.01$). Likewise, there was a significant depletion in the $\delta^{15}N$ of invertebrates between seasons (Independent T-test: t = 3.4, $p < 0.01$) whereas the C_4 plants remained relatively the same between seasons (winter: -0.2 ± 2.1‰; n = 5 and summer: -0.2 ± 1.5‰; n = 5; Figure 2).

The whole blood of forest birds was significantly depleted in $\delta^{15}N$ in summer compared to winter (Independent T-test; t = 3.8; $p < 0.01$). There was a significant positive relationship between $\delta^{13}C$ and $\delta^{15}N$ in the whole blood of forest birds in winter (Linear regression: $r^2 = 0.5$, y = -28.8‰ + 0.8x; $p < 0.01$) and summer (Linear regression: $r^2 = 0.6$, y = -28.5‰ + 0.9x; $p < 0.01$; Figure 2). There was a significant positive correlation between $\delta^{13}C$ and $\delta^{15}N$ in forest specialists in summer ($r = 0.7$; $p < 0.05$), but not in the $\delta^{13}C$ and $\delta^{15}N$ of forest generalists or forest visitors.

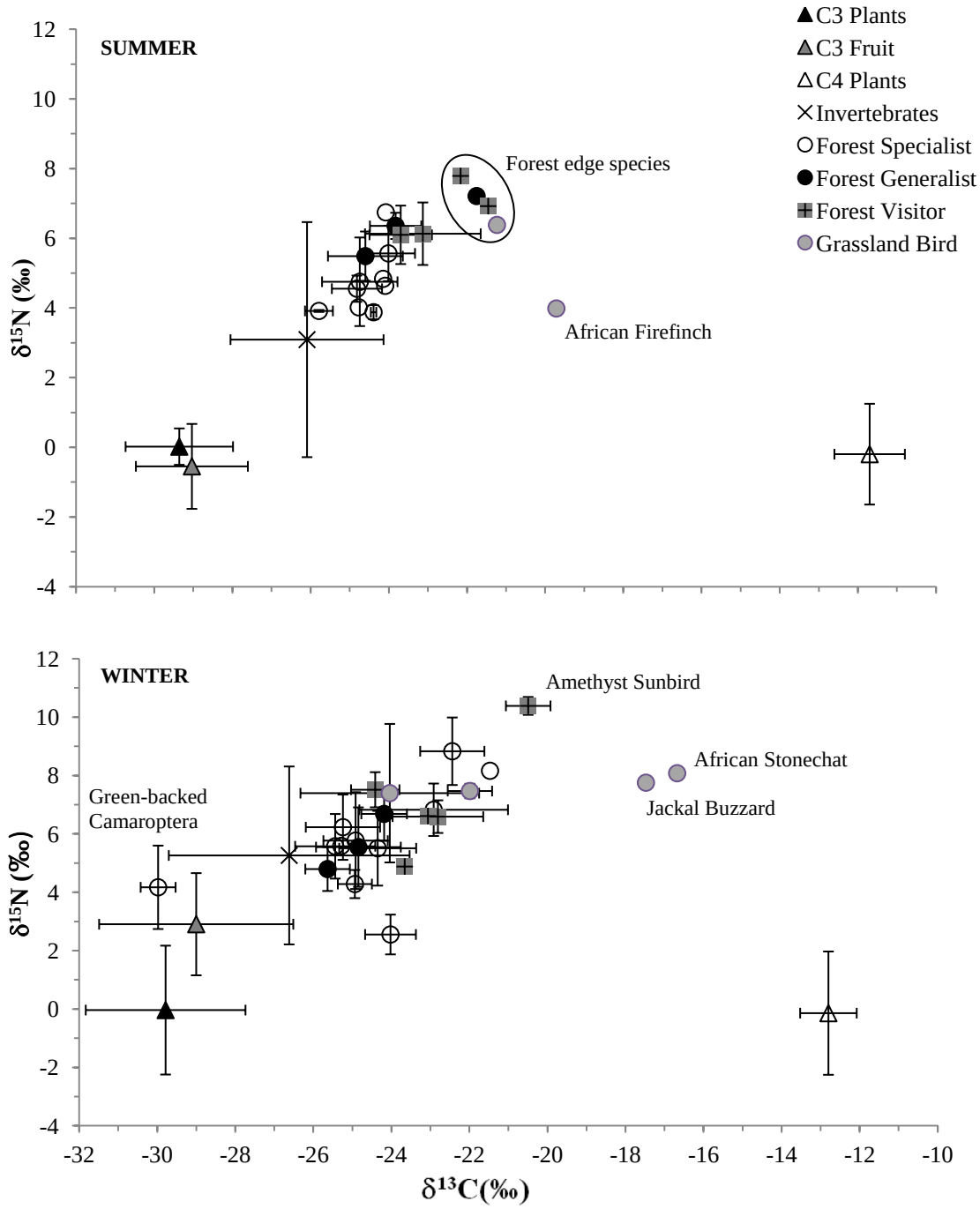

Figure 2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic depiction of forest birds in winter and summer in New Forest, South Africa. Whole blood of forest specialists (winter n = 11, summer n = 9), forest generalists (winter n = 3, summer n = 3), forest visitors (winter n = 5, summer n = 4), and grassland species (winter n = 4, summer n = 2). C_3 plants (winter n = 19, summer n = 24 excluding fruit), C_3 fruit (winter n = 13, summer n = 11), C_4 plants (winter n = 5, summer n = 5), and whole invertebrates (winter n = 51 representing 15 orders, summer n = 52 representing 17 orders) are also shown. Standard deviation is given where > 2 individuals sampled per species.

4.4.2. C_3 contribution to forest birds

There was significant inter-specific variation in blood $\delta^{13}C$ in winter (Kruskal-Wallis Test: $H_{5,81} = 20.5$; $p < 0.01$; range -16.7 to -30.0‰) and summer (Kruskal-Wallis Test: $H_{15,98} = 55.4$; $p < 0.01$; range -19.7 to -25.8‰). Of the 23 bird species in winter, 39% (n = 9) had ≥ 70% contribution of C_3 plants to their diet but in summer 33% (n = 6) of bird species, had ≥ 70% contribution of C_3 plants to their diet (Table 1). All of these species were either forest specialists or forest generalist, excluding Cape White-eye *Zosterops virens*, which is a forest visitor. Further, 87% (n = 20) of forest birds had ≥ 50% contribution of C_3 plants to their diet in winter but this increased to 94% (n = 17) of birds that had ≥ 50% contribution of C_3 plants to their diet, all of which were either forest specialists or forest generalists (Table 1).

Of the 13 species sampled in both seasons, the proportion of C_3 in the diet increased for three species only (23%), Chorister Robin-Chat *Cossypha dichroa*, Cape Robin-Chat *Cossypha caffra*, and Southern Double-collared Sunbird *Cinnyris chalybeus* in summer (Table 1). However, the proportion of C_3 in the diet decreased for the remaining 10 species (77%) but remained above 65% for all forest specialists and forest generalists, excluding African Dusky Flycatcher *Muscicapa adusta* (Table 1).

The range in carbon isotope values was generally greater in birds sampled in winter than birds in summer, particularly in species that had < 70% C_3 contribution to the diet.

Table 1. Contribution(%) of C_3 carbon sources to the whole blood of forest bird species in winter and summer (Isoerror two-endpoint mixing model; Philips and Gregg 2001). Birds are ordered from highest to lowest C_3 contribution (%) in winter (*Note: Standard Error is < 0.05 in all cases). The range in blood carbon is also given (R). Forest specialists (Oatley 1989) are bold, forest generalists (F), forest visitors (f), and grassland birds (G). Feeding guilds (FG) include insectivore (I), omnivore (O), nectarivore (N), and frugivore (F).

		Winter				Summer		
Bird Species	**FG**	**n**	**$\delta^{13}C$‰**	**%C_3**	**R‰**	**n**	**$\delta^{13}C$‰**	**%C_3**	**R‰**
Green-backed Camaroptera *Camaroptera brachyura*	I	3	-30.0 ± 0.1	100	0.6	3	-25.8 ± 1.1	78	0.5
Sombre Greenbul *Andropadus importunus* [F]	F	9	-25.6 ± 0.2	77	1.6	13	-24.6 ± 0.3	71	3.0
Bar-throated Apalis *Apalis thoracia*	I	13	-25.4 ± 0.5	76	2.9	12	-24.7 ± 0.1	72	3.3
White-starred Robin *Pogonocichla stellata*	I	7	-25.2 ± 0.2	75	1.7	10	-24.8 ± 0.0	72	1.8
Dark-backed Weaver *Ploceus bicolor*	I	1	-25.3	75	-	1	-24.1	68	-
Yellow-throated Woodland-Warbler *Phylloscopus ruficapilla*	I	5	-24.9 ± 0.1	73	1.0	2	-24.4	70	0.1
Southern Boubou *Laniarius ferrugineus* [F]	O	4	-24.9 ± 0.6	73	2.4	-	-	-	-
Bush Blackcap *Lioptilus nigricapillus*	F	-	-	-	-	1	-24.8	72	-
Cape Batis *Batis capensis*	I	7	-24.4 ± 0.2	70	2.2	14	-24.0 ± 0.1	68	2.1
Cape White-eye *Zosterops virens* [f]	O	11	-24.4 ± 0.1	70	2.1	42	-23.7 ± 0.2	66	3.3
Olive Thrush *Turdus olivaceus* [F]	I	11	-24.2 ± 0.3	69	1.9	-	-	-	-
Lemon Dove *Aplopelia larvata*	G	4	-24.0 ± 0.5	68	1.2	-	-	-	-
Drakensberg Prinia *Prinia hypoxantha* [f]	I	3	-24.0 ± 0.1	68	4.0	3	-22.2 ± 0.2	58	0.0
Terrestrial Brownbul *Phyllastrephus terrestris* [F]	I	-	-	-	-	2	-23.8	67	0.9
Black-headed Oriole *Oriolus larvatus* [f]	I	1	-23.7	66	-	-	-	-	-
Fork-tailed Drongo *Dicrurus adsimilis* [f]	I	1	-23.2	63	-	-	-	-	-

Bird Species	FG	Winter				Summer			
		n	$\delta^{13}C‰$	$\%C_3$	R‰	n	$\delta^{13}C‰$	$\%C_3$	R‰
Yellow-breasted Apalis *Apalis flavida* [f]	I	1	-23.1	62	-	-	-	-	-
Chorister Robin-Chat *Cossypha dichroa*	O	9	-22.9 ± 0.1	61	4.4	2	-24.1	69	0.0
Cape Robin-Chat *Cossypha caffra* [f]	O	20	-22.8 ± 0.2	60	4.0	7	-23.1 ± 0.4	63	3.7
Lazy Cisticola *Cisticola aberrans* [G]	I	3	-22.6 ± 0.0	59	0.8	2	-21.2	52	0.0
Southern Double-collared Sunbird *Cinnyris chalybeus*	N	8	-22.4 ± 0.1	58	2.4	1	-24.1	68	-
African Dusky Flycatcher *Muscicapa adusta* [F]	I	-	-	-	-	3	-21.8	55	0.0
African Paradise-Flycatcher *Terpsiphone viridis* [f]	I	-	-	-	-	1	-21.5	54	-
African Goshawk *Accipiter tachiro*	C	1	-21.5	52	-	-	-	-	-
Amethyst Sunbird *Chalcomitra amethystina* [f]	N	2	-20.5	46	0.8	-	-	-	-
African Firefinch *Lagonosticta rubricata* [G]	G	-	-	-	-	1	-19.7	44	-
Jackal Buzzard *Buteo rufofuscus* [G]	C	1	-17.5	28	-	-	-	-	-
African Stonechat *Saxicola torquatus* [G]	I	1	-16.7	23	-	-	-	-	-

4.4.3. Blood nitrogen and dietary shifts

Overall, there was significant inter-specific variation in blood $\delta^{15}N$ between forest birds in winter (Kruskal-Wallis Test: $H_{5,81} = 26.2$; $p < 0.01$) and summer (Kruskal-Wallis Test: $H_{15,98} = 62.7$; $p < 0.01$). In addition, the range in blood nitrogen was higher in forest birds in winter (range = 8.8‰) than summer (range = 4.5‰). Although many of the species sampled in winter were not re-sampled in summer (see Table 1 for species reference), several birds that were re-sampled in summer had relatively depleted blood nitrogen (Table 2). Therefore, to account for seasonal differences in plant $\delta^{15}N$, the trophic level (TL) equation was used to assess seasonal dietary shifts within species (Table 2). The Southern Double-collared Sunbird *Cinnyris chalybeus* (a nectarivore) was at the highest TL in winter, but decreased in summer where Drakensberg Prinia *Prinia hypoxantha* (an insectivore) was at the highest TL (Table 2). The frugivore and omnivores included insects in their diet in both seasons and therefore had $\delta^{15}N$ values similar to those of other insectivores (Table 2). Most species decreased in TL from winter to summer, except for Cape Batis *Batis capensis*, which remained the same (Table 2).

Table 2. The $\delta^{15}N$ values of whole blood, $\delta^{15}N$ range (R), and trophic levels (TL; equation 2) of forest birds recorded in both winter and summer in New Forest, South Africa. Birds are ordered from highest to lowest trophic level in winter.

		Winter					Summer				
Bird Species	**FG**	**n**	**$\delta^{15}N$‰**	**R‰**	**TL**	**FM**	**n**	**$\delta^{15}N$‰**	**R‰**	**TL**	**FM**
Southern Double-collared Sunbird *Cinnyris chalybeus*	N	8	8.8 ± 1.2	3.8	3.9 ± 0.4	-	1	6.7	-	3.2	-
Drakensberg Prinia *Prinia hypoxantha* [f]	I	3	7.4 ± 2.4	4.7	3.4 ± 0.8	IM	1	7.8	-	3.5	I
Lazy Cisticola *Cisticola aberrans* [G]	I	3	7.5 ± 0.2	0.3	3.4	I	2	6.4	0.0	3.1	I
Cape White-eye *Zosterops virens* [f]	O	11	7.5 ± 0.6	2.3	3.4 ± 0.2	IM	42	6.1 ± 0.8	2.9	3.0 ± 0.2	PI
Chorister Robin-Chat *Cossypha dichroa*	O	9	6.8 ± 0.9	2.3	3.2	M	2	4.8	0.0	2.6	I
Cape Robin-Chat *Cossypha caffra* [f]	O	20	6.6 ± 0.6	2.1	3.1 ± 0.2	IP	7	6.1 ± 0.9	2.3	3.0 ± 0.3	IP
White-starred Robin *Pogonocichla stellata*	I	7	6.2 ± 1.1	2.2	3.0	I	2	4.6	1.2	2.5	I
Bar-throated Apalis *Apalis thoracica*	I	13	5.6 ± 1.1	3.6	2.8 ± 0.4	I	12	4.8 ± 1.3	3.8	2.5 ± 0.4	I
Dark-backed Weaver *Ploceus bicolor*	I	1	5.6	-	2.9	I	1	4.6	-	2.4	-
Cape Batis *Batis capensis*	I	7	5.5 ± 1.3	3.5	2.8 ± 0.4	I	14	5.6 ± 0.8	2.1	2.8 ± 0.3	I
Sombre Greenbul *Andropadus importunus* [F]	F	9	4.8 ± 0.8	2.2	2.6 ± 0.3	P	13	5.5 ± 0.7	2.4	2.8 ± 0.2	PI
Yellow-throated Woodland-Warbler *Phylloscopus ruficapilla*	I	5	4.3 ± 0.5	1.1	2.4	I	2	3.9	0.3	2.2	I
Green-backed Camaroptera *Camaroptera brachyura*	I	3	4.2 ± 1.4	2.0	2.4 ± 0.5	-	3	3.9	0.04	2.3 ± 0.01	I

[1]Forest specialists (Oatley 1989) are bold, forest generalists (F), forest visitors (f), and grassland birds (G) are indicated. Feeding guilds (FG) include insectivore (I), omnivore (O), nectarivore (N), and frugivore (F). Faecal matter content (FM) is based on the presence of invertebrate matter (I), plant material (P), or a mixture of the invertebrate and plant material (M) within each faecal sample of an individual.

4.5. Discussion

4.5.1. Isotopic community structure

There was a positive relationship between $\delta^{13}C$ and $\delta^{15}N$ in the whole blood of forest birds in both winter and summer. This was potentially due to the stepwise enrichment of $\delta^{13}C$ and $\delta^{15}N$ with an increase in trophic level (Bearhop *et al.* 2002; Post 2002). As expected, a true granivore, the Lemon Dove *Aplopelia larvata*, had the lowest $\delta^{15}N$ signature in winter (see Symes and Woodborne 2009). However, a nectarivore, Amethyst Sunbird *Chalcomitra amethystina*, had the most enriched $\delta^{15}N$ in the dry season, followed by Southern Double-collared Sunbird *Cinnyris chalybeus*. The whole blood of both nectarivores was enriched in $\delta^{15}N$ compared to the African Goshawk *Accipiter tachiro*, a predator of other birds in the forest (Hockey *et al.* 2005). Although true granivores or frugivores were not sampled in summer, the positive relationship between $\delta^{13}C$ and $\delta^{15}N$ was maintained. This finding is different from a study done in the tropical forests in Los Tuxtlas, Veracruz, Mexico (Herrera *et al.* 2003) and another in the Afromontane forests in the Soutpansberg, South Africa (Symes and Woodborne 2009). The isotopic values in both studies clustered together with no obvious relationship between $\delta^{13}C$ and $\delta^{15}N$. The study in the Soutpansberg forest, however, used feather samples and not whole blood to depict the isotopic community. Feathers provide information on dietary intake and assimilation from the time the feathers were grown, and not necessarily assimilation at the time of sampling (Bearhop *et al*. 2002). Therefore, the isotopic depiction is a consequence of assimilation at different times over the last few months prior to sampling and not a snapshot of time. It is interesting that the pattern between $\delta^{13}C$ and $\delta^{15}N$ in the whole blood of forest birds in Mexico was different from this study but similar to Symes and Woodborne (2009). However, the isotope data were collected over a year in the Mexican forests and pooled together which may explain the similar result to Symes and Woodborne (2009).

Dietary patterns differed between forest specialists, generalists, and visitors. In winter, it would appear that all forest birds relied quite extensively on the forest for their dietary requirements because forest specialists, forest generalists, forest visitors and grassland birds all had similar isotopic values. In summer, however, there was distinct clustering between forest specialists and generalists as well as between known forest edge species in summer. These edge species were Lazy Cistola *Cisticola aberrans*, Drakensberg Prinia *Prinia*

hypoxantha, African Paradise-Flycatcher *Terpsiphone viridis*, and African Dusky Flycatcher *Muscicapa adusta* (see Skead 1964; Hockey *et al.* 2005). The general lack of isotopic distinction between forest birds in winter may have indicated that food resources were quantitatively limited in the dry season, and therefore birds became generalist feeders to fulfil dietary requirements. In contrast, food resources may no longer have been limiting in summer, and so birds preferentially select desired food resources. These findings were similar to behavioural studies done in New Forest (Chapter 3).

4.5.2. C_3 contribution to the diet of forest birds

The high inter-specific variation between birds, and the greater range in $\delta^{13}C$ in several forest birds, indicated a high variance in the basal food source in winter (Herrera *et al.* 2003). Even so, the C_3 contribution to the diet of forest birds was greatest in winter compared to summer, particularly in forest specialists and forest generalists. Even though the proportion of C_3 carbon in the diet decreased for most species from winter to summer, the proportion of C_3 in the whole blood of forest specialists and generalists remained above 65%. Possibly, because forest specialists and forest generalists are more dependent on the forest system for dietary requirements than forest visitors are (Oatley 1989; Bennun *et al.* 1996). Further, the high contribution of C_3 to the diet in forest specialists and forest generalists and the low proportion of C_4 in the diet are because C_3 is the dominant food source in the forest (Herrera *et al.* 2003; Herrera *et al.* 2006). Forest openings have a different plant community from the surrounding forest because they contain a greater number of grass species and sedges and therefore some plant species are isotopically enriched compared to the C_3 plants in the general forest environment. Several of these species flowered in summer, which may have been a source to both insects and birds (SLS *pers. obs.*). The varying proportions of C_4/CAM plants in the diet of forest birds could therefore be due to direct dietary selection of plants that grow in the open areas of the forest or from the surrounding grassland, or indirect intake from invertebrates that forage on these plants.

Invertebrate diversity increased from winter to summer due to the increased availability of food resources in the forest canopy, on the forest floor, and in the forest openings (Chapter 2&3). If C_4 plants also contributed to the diet of invertebrates as well as C_3 plants, then insectivores, such as Green-backed Camaroptera *Camaroptera brachyura* and White-starred Robin *Pogonocichla stellata* that fed on these invertebrates would reflect this. Likewise, frugivores, such as Sombre Greenbul *Andropadus importunus* increased

invertebrate intake into the diet in summer (Chapter 3). Therefore, if these species are also eating invertebrates that forage on C_4/ CAM plants, the proportion of C_3 in the diet would also be reduced.

4.5.3. Blood nitrogen and dietary shifts

The nitrogen signature of the forest birds in summer were depleted relative to the winter forest birds. However, this may have been because the nitrogen signature of the food base, particularly C_3 fruit and invertebrates, was significantly depleted in summer. The mean $\delta^{15}N$ values for the combined winter and summer C_3 fruit (1.8 ± 2.7‰; n = 25; range -2.4 to 9.8‰) and invertebrates (4.1 ± 3.4‰; n = 73; range -3.3 to 14.5‰) values are strikingly similar to the mean values from tropical forests in Los Tuxtlas, Veracruz, Mexico (Herrera *et al.* 2003).

There was high inter-specific variation in blood nitrogen, which indicated a large variation in trophic structure in the forest bird community in both seasons (Herrera *et al.* 2003). The range in blood nitrogen was higher in forest birds in winter relative to summer. This was because of the presence of the ground-foraging granivores and the extreme enriched nitrogen signatures of the sunbirds in winter, as stated previously. The differential use of nitrogen sources between species may suggest that species respond differently to seasonal changes in food availability (Herrera *et al.* 2005). Seasonal variation in food availability may stimulate nomadism in some bird species between areas (Poulin *et al.* 1994) as well as the extent to which these resources are utilised by birds (Herrera *et al.* 2005). For example, many of the granivores, frugivores, and nectarivores left the forest in summer to forage elsewhere, whilst insectivores and omnivores increased in abundance in the forest in summer (Chapter 2). That is why the majority of species that were compared between seasons were insect-eaters.

The insectivores had the greatest range in blood nitrogen values compared to other guilds, including the omnivores. This is surprising as omnivores tend to diet-switch between seasons depending on the primary food resource available (Koen 1992) whereas insectivores do not. The $\delta^{15}N$ signature and trophic level of the Sombre Greenbul (a frugivore), and Chorister Robin-Chat *Cossypha dichroa* and Cape Robin-Chat *Cossypha caffra* (both omnivores) indicated a predominantly insectivorous diet in summer. All three species had a mixed diet of fruit and invertebrates, particularly in winter where fruit was more abundant (Chapter 2&3). The $\delta^{15}N$ signature of omnivores became depleted in summer whereas the $\delta^{15}N$ signature and trophic level of the Sombre Greenbul increased in blood nitrogen in

summer. This may have been due to an increase in invertebrate intake in summer, as observed in the faecal matter and in the field (Chapter 3). In several instances where trophic level decreased in one season relative to another, plant material was recorded in the faecal matter, such as Drakensberg Prinia, Cape White-eye *Zosterops virens*, and Sombre Greenbul. In other instances where the contents of the faecal matter did not change, it is possible that there was a change in resource selection within a food-type. For example, all insectivores, except for Drakensberg Prinia and Cape Batis, decreased in trophic level from winter to summer even though these species exclusively ate insects in both seasons. Seasonal changes in nutritional requirements, particularly of protein, may determine food selection of differing nutritional value (Herrera *et al.* 2005). Dietary modification or complete switching in response to seasonal abundance in either fruit, flowers, or invertebrates has been recorded in forests elsewhere (Herrera *et al.* 2003; Herrera *et al.* 2005; Herrera *et al.* 2006).

Quantitative limitation in food availability is not the only explanation for isotopic changes in bird species between seasons. The Southern Double-collared Sunbird forages on insects in addition to their preferred food choice (Koen 1988b; Koen 1992). The inclusion of invertebrates in the sunbird diet may explain the high $\delta^{15}N$ signature of the sunbirds in winter (Symes and Woodborne 2009). However, this may have also been due to nitrogen recycling of endogenous proteins when exogenous proteins may have been deficient in the system (Symes and Woodborne 2009). Both *Halleria lucida* and Red Hot Pokers *Kniphofia* spp. produce high quality, concentrated nectar sources in small volumes (Frost and Frost 1980; Brown and Downs 2010). However, sunbirds, particularly Southern Double-collared Sunbird, foraged on invertebrates in winter and on the flowers on *Halleria lucida* (‰^{15}N: -0.6‰; n = 1), but were only observed foraging on *Kniphofia* spp. (‰^{15}N: 0.01‰; n = 1) in summer (Chapter 3). This does not mean that sunbirds did not forage on insects, but possibly were only observed drinking nectar because they did this more frequently in summer than in winter. Spiders in particular had a high $\delta^{15}N$ value in winter (7.1 ± 0.7‰; n = 7) compared to summer (4.9 ± 1.9‰; n = 5), a potential food source that sunbirds may have targeted. Therefore, although *H. lucida* produced high quality, readily available nectar, sunbirds still need to increase invertebrates in winter in preparation for the breeding season (Fogden 1972; Wolf 1975; Symes and Woodborne 2009). Many factors influence isotopic signatures of tissues including metabolic processes and nutrient stress, which may affect the $\delta^{15}N$ signature of some species more than other species (Hobson and Clark 1992b; Hobson and Clark 1992b; Vanderklift and Ponsard 2003), and these influences are species-specific. Food selection and

metabolic processes may be a more parsimonious explanation for isotopic variation within guilds and between species.

4.6. Conclusion

Seasonal differences in the dietary patterns of forest birds were driven by food selection of forest birds because preferred food resources were more readily available in summer compared to winter, and so birds became more specific in resource selection. Forest birds, particularly forest specialists and generalists, were heavily dependent on the forest environment as a food source, particularly in winter. Forest visitors and grassland birds intermixed with forest specialists and generalists in the forest in the dry season and had a relatively high contribution of C_3 to their diet in winter. This indicated that the forest became a refuge for these species when food resources were limiting. Quantitative limitation in food resources determines the trophic position of the species within the community where birds select for the most abundant resource in a season. However, qualitative limitation may have been a more parsimonious explanation in birds, such as nectarivores that increased invertebrate intake when the nutritional requirements were not met from their preferred nectar resource. There was a positive relationship between $\delta^{13}C$ and $\delta^{15}N$ in the whole blood of forest birds in both winter and summer potentially due to an increase in trophic level. Several studies pool isotopic data collected over several seasons and therefore do not show the same pattern as the data have here. We recommend that seasons be analysed separately for further insight into the dietary patterns of forest birds.

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Chapter 5: Importance of forest patches to birds

5.1. Discussion and Conclusion

This was the first study in South Africa to classify forest birds further, into forest generalists and forest visitors (as classified by Bennun *et al.* 1996) in addition to forest specialists. The classifications were important because they provided further insight into the functional dynamics of the forest bird community as well as forest condition and value for conservation (Bennun *et al.* 1996). New Forest, for example, held a high proportion of forest specialists, which demonstrated the importance of medium-sized forest patches to the conservation of these disturbance-sensitive species (Oatley 1989). Therefore, a review of forest bird classification into the various categories is needed because forest dependency varies within and between bird species depending on the surrounding matrix. Furthermore, it is important to classify birds according to dependency on a forest-type or forest sub-type in South Africa to standardise the classification of birds to avoid discrepancies in the future.

Forest patches are useful in bird community studies because they have a different floral and faunal community from the surrounding non-forest matrix (Geldenhuys and MacDevette 1989). Due to the composition of plants in the Afromontane forest patch, there were structural and functional changes in forest vegetation between the dry (winter) and wet (summer) seasons (Chapter 2&3). There was an increase in vegetation cover in summer due to the greening of deciduous canopy plants, such as *Celtis africana* as well as growth of annuals on the forest floor (Chapter 2&3). There was also a seasonal change in general food availability as well as in the vertical distribution of food where canopy trees, such as *Podocarpus latifolius* and *Celtis africana* produced abundant fruit and *Halleria lucida* was the dominant flowering plant in winter, but understory plants produced the highest relative abundance of fruit and flowers in summer (Chapter 2). The flowering of forest floor annuals as well as the greening of canopy plants provided additional food to invertebrates, which contributed to the increase in invertebrate diversity in the wet season. The change in flowering and fruiting phenology between seasons as well as a change in the vertical stratification of food influenced both the community dynamics and the foraging ecology of birds.

Bird communities in Afromontane patches were not static over time (Chapter 2). Although some bird species were present in the forest all year round, other birds made local movements, altitudinal migrations, or latitudinal migrations to breed or forage elsewhere between seasons (Chapter 2). Further, birds that remained were not equally abundant between

winter and summer and appeared to have a relationship with food availability. This was particularly obvious when birds were assessed using feeding guilds. The bias towards gregarious frugivores and nectarivores in winter was most likely due to the conspicuous fruiting and flowering of canopy trees (Chapter 2). Frugivores and nectarivores were more often limited in food availability (Newton 2003; Symes *et al.* 2002) than insect-eating guilds (Geldenhuys 1989) because of the strong seasonal flower and fruit phenology in forests (Geldenhuys 1989; Koen 1992; Wirminghaus *et al.* 2001; Borghesio and Laiolo 2004). The species most likely to track food spatially to areas of abundance were the forest generalists or visitors that are not completely dependent on forest. A reduction in conspicuous flowers and fruit in canopy trees in summer, and the simultaneous increase in invertebrate diversity and fruit in the understory in the wet season caused a functional shift in the forest bird community. Nectarivores, frugivores, and granivores decreased in abundance and biomass in summer but insectivores and omnivores increased in the forest. Plant composition of a forest is therefore important to the composition, richness, and function of forest birds (Holmes 1986), which is dynamic due to the periodic influx of bird species into the forest in response to changes in food. Understanding the drivers of compositional change in a forest patch can contribute the connectedness between forest avifauna can be maintained between patches in a forest complex.

Factors that determine bird presence and diversity in a forest are largely species-specific and the level of importance of each factor vary over a space and time (Newton 2003). The spatial movements of birds between forests and non-forest environment have important implications for the dispersal of both forest plants and exotic plants. Thick-billed Weavers *Amblyospiza albifrons,* for example, entered the forest in winter to forage on fruit provided by canopy trees like *Celtis africana* or climbers, such as *Scutia myrtina* but exited the forest in the wet season to breed in reed beds (Hockey *et al.* 2005). The movement of Thick-billed Weavers between forest patches may have been an important disperser of *Celtis africana* (Neushulz *et al.* 2011). The Cape White-eye *Zosterops virens* (forest visitor) and the African Olive-Pigeon *Columba arquatrix* (forest generalist) foraged in both forest and non-forest (e.g. surrounding plantations) areas, and the African Olive-Pigeon fed extensively on invasive species like *Solanum* (Skead 1964; Oatley 1984). American Bramble *Rubus cuneifolius* (exotic species) grows in dense clusters in the grassland and produces a sweet fruit in summer, the seeds of which were present in the faecal matter of Cape White-eye. Likewise, Cape Robin-Chat *Cossypha caffra* (forest visitor) was observed eating fruit from *Pyracantha*

angustifolia (exotic species) in the forest. Many attempts are currently being made to remove Bramble from the surrounding grassland and from the openings within the forest. Many of the invader species, such as Bramble, only establish in forest openings where there is sufficient light. Therefore, forest management plans should aim to reduce wood removal from forests and promote forest regeneration particularly in disturbed areas.

In addition to the seasonal movement of birds out of the forest, birds also dealt with changes in food availability through behavioural adaptations in foraging ecology. Other studies have demonstrated that resources are not equally abundant between seasons (Fogden 1972; Murali and Sukumar 1994; Borghesio and Laiolo 2004), and therefore are limiting in one season or another. This study, however, demonstrated that resource limitation in a season is species-specific (Chapter 3). Insectivores, for example, were quantitatively limited by invertebrate availability in winter whereas nectarivores were potentially qualitatively limited due to additional protein requirements of these birds to prepare for the breeding season (Fogden 1972; Wolf 1975; Wolf and Wolf 1976; Symes and Woodborne 2009). The manner in which species cope with resource limitation varies between species. For example, insectivores foraged over a broader vertical range in winter and exploited a wider range of invertebrates whereas nectarivores expanded their dietary range to include invertebrates in their diet. However, because of the mass fruit contribution to the system by canopy trees, such as *Podocarpus latifolius* as well as the diversity of ripe fruits provided by climbers like *Coccinia palmata* and several understory plants, frugivores, such as the Dark-capped Bulbul *Pycnonotus tricolor* and Sombre Greenbul *Andropadus importunus* were not limited in either quantity or quality of food. These species also supplemented their diet with invertebrates, regardless of season. Seasonal limitation in fruit availability may however become important in strict frugivores, such as the Knysna Turaco *Turaco corythaix* that is also a forest specialist, and less likely to forage over a broad spatial range in search of food because it is also a canopy frugivore (Koen 1988). Therefore, when resources were limited, several bird species became generalist in food selection and forage height and range to fulfil nutritional requirements (Chapter 3).

Stable isotope analysis provided additional and valuable support to the field observations in foraging behaviour (Chapter 4). The $\delta^{13}C$ and $\delta^{15}N$ whole blood values of birds indicated that forest visitors and grassland birds relied on food sources from both the C_3 and C_4 environments in winter. However, in summer there appeared to be an isotopic clustering of forest specialists and forest generalists, which were more dependent on the forest environment. Likewise, there was clustering of forest visitors and grassland species,

known to be forest edge-utilizers (see Skead 1964; Hockey *et al.* 2005). Both forest specialists and forest generalists consistently had a high contribution of C_3 to their diets in both seasons, not only indicating a high level of dependency on the forest system but also confirmed the categorisation of these species as specialist or generalist as determined by field observations (see Oatley 1989; Bennun *et al.* 1996). Carbon and nitrogen stable isotope analysis has added substantial value to the behaviours observed in New Forest, and has demonstrated a dynamic between the forest and grassland environments.

The assessment of ecological requirements, such as food availability and structure, will have practical conservation importance in drawing attention to bird species that need to be protected (Dowsett-Lemaire and Dowsett 1984). These interpretations may also assist in better decision making processes regarding the conservation of indigenous forest in South Africa because although indigenous forests appear to be well conserved in southern Africa, patches are generally poorly managed (Lawes and Eeley 2000). Furthermore, forests are not equally represented because scarp and coastal lowland forests are better represented in conserved areas than Afromontane forest (Eeley *et al.* 2001). Forest specialists are more vulnerable to anthropogenic disturbance than forest generalist species (Neuschulz *et al.* 2011). Therefore, the idenfication of these birds in a forest patch may be valuable in the selection of certain forests for conservation because these species are most likely to diappear in heavily disturbed areas (Oatley 1989; Neuschulz *et al.* 2011). Forests are not only an important refuge to forest specialists for survival, but also to birds that are seasonally limited by food availability. Therefore, the understanding and conservation of processes is of the utmost concern for the support and maintenance of bird diversity and compositional functional dynamics in forests over time (Geldenhuys and MacDevette 1989; Castley and Kerley 1996; Bennun *et al.* 1996; Midgley *et al.* 2003).

5.2. References

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Glossary of terms

Altitudinal migrant: Seasonal migration in response to environmental conditions (Hockey *et al.* 2005).

Bite: A bird acquires a portion of a large fruit by biting it and swallowing pieces at a time rather than the whole fruit (modified from Foster 1987).

Canopy stratum (canopy): Taller, larger-stemmed trees whose canopies are > 8m.

Carnivore: A predominant diet of vertebrates.

Community: The assemblage of co-occurring species in an area, which is dynamic over space and time (Wiens 1989).

Discrimination factor: The difference in isotopic composition between diet and an organism's tissue (Newsome *et al.* 2012) using the following equation:

$\Delta = ‰^{15}N_{consumer} - ‰^{15}N_{diet}$.

Ecological niche: The set of environmental conditions in an ecosystem in which a species exists (Hutchinson 1957; Root 1967).

Forest generalist: Bird species that are partly dependent on the forest environment, particularly as a breeding site, but commonly recorded at the forest edge or other wooded environments rather than the forest interior (Bennun *et al.* 1996).

Forest visitor: Bird species that are not dependent on the forest ecosystem for survival and are commonly recorded in other vegetation-types (Bennun *et al.* 1996).

Forest-specific species or forest specialist: Bird species that are completely dependent on the forest environment for reproduction and survival (Oatley 1989).

Fractionation: A change in the isotopic signal between diet and consumer tissues. This effect is due to both selective biochemical assimilation of dietary components that have different isotopic signatures, and by isotopic discrimination (Hobson and Clark 1992b).

Frugivore: Predominantly consume whole fruit, but do eat invertebrates.

Gause Principle (Competitive Exclusion Principle): Species that cannot compete successfully for a resource will be extirpated from the area (Gause 1934; Hardin 1960).

Glean: A perched bird picks stationary prey from a nearby substrate where no flight is involved for either bird or its' prey, usually to capture invertebrate prey.

Granivore: Removes pulp from fruit and consumes the seed only or eat seeds from plants, such as grass.

Ground stratum (ground): Leaf litter and soil at 0 m**.**

Guild: A group of species that exploit the same category of resources in a similar manner (Root 1967; Simberloff and Dayan 1991).

Hang: A bird hangs upside down and may glean, tear apart, or manipulate a substrate in some way to access a food resource, either invertebrates or fruit.

Hawk: A bird flies out from a perch, up or down, to capture air-borne prey to capture invertebrate prey.

Hover: A bird flies out to snatch prey, (invertebrates or fruit), from a substrate, excluding air. It may pause and hover shortly at a substrate or snatch the prey from a substrate as it passes.

Insectivore: A predominant diet of invertebrate matter.

Local seasonal movements: Species move between local areas for breeding purposes or to track food availability between seasons (Hockey *et al.* 2005).

Migrant: Overwinter in the Afrotropics or elsewhere and return in summer (Hockey *et al.* 2005). Species that return to southern Africa to breed in the summer are known as breeding migrants.

Nectarivore: Predominantly drink nectar from flowers, but do eat invertebrates.

Omnivore: Bird species that consume a mixed diet of invertebrate and vegetable matter.

Peck: A bird walks quickly over the ground and picks seeds from the surface as it moves (modified from Koen 1988).

Pluck: A bird thrusts its head forward to acquire a fruit and swallows it whole (Foster 1987).

Pounce: A predatory bird captures prey with its feet as it lands on a substrate, typically the ground.

Probe: A bird inserts their beak into a hole or crack in wood or bark in search of grubs, or flowers for nectar.

Resident: Species that remain in the same area throughout the year (Hockey *et al.* 2005).

Sift: A bird flicks through leaf litter with its beak in search of food, usually in search of invertebrates or fruit.

Stable isotope: Elements that have the same number of protons and electrons but differ in the number of neutrons (Inger and Bearhop 2008).

Understory: A vertical layer between 0 and 8 m where shorter, thin-stemmed trees dominate.